Larval fish ecology - adaptations and physical linkages

Munk, Peter

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Peter Munk
National Institute of Aquatic Resources – DTU Aqua
Technical University of Denmark

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Kgs. Lyngby, den 24. maj 2016

Anders O. Bjarklev

Rektor

/Henrik C. Wegener

Prorektor

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Kgs. Lyngby, 24 May 2016

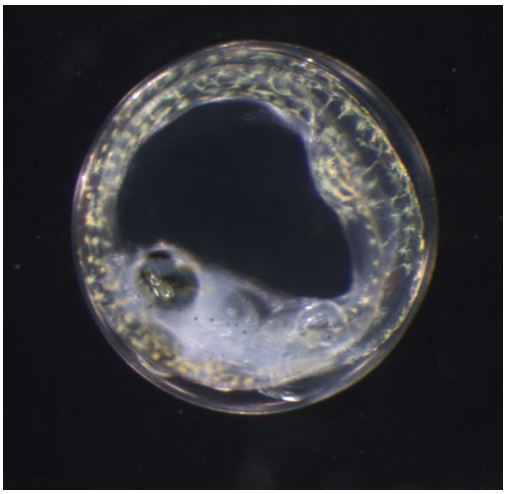
Anders O. Bjarklev

President

/Henrik C. Wegener
Provost

Foreword

My research and this thesis are directed towards improved understanding of key processes in the larval life of fish. A fish larva is only one among many types of organisms drifting freely in the sea as plankton, and the duration of the larval stage is short compared to the entire life of the fish. However, I hope that I can demonstrate here that insight into the larval life of fish, into the constraints and opportunities they meet and into the adaptations they show, are essential parts of our understanding of the functioning of the plankton ecosystem and of the life cycles of fish. As a research topic, the larval life of fish is at the intersection of a series of classical research areas. Consequently it covers a wide range of disciplines and it demands extensive cooperation among scientists. The breadth of the research field will become apparent in this thesis which covers methods ranging from small scale laboratory observations of behavior to multidisciplinary cruises on very large scales.



Just before starting life as larvae. A colorful plaice embryo inside the egg. Own photo .

I was hooked by the fish larvae early in my career. Already during the work for my master's degree, the life of fish larvae became a focus for my research career. During some hectic months in 1978, I successfully reared turbot larvae for the first time in Denmark and analyzed their progress in the then new facilities at Vognporten in Charlottenlund. During that work I received superb support and guidance from Erik Hofmann and Jan E. Beyer, and when the first phases of the thesis work were focused on aquaculture aspects of larval rearing, the final project produced new, exciting results about patterns of growth. I was lucky to get the opportunity to continue in fishery science at Danmarks Fiskeri og Havundersøgelser (DF&H), and here I was part of a group of young scientists who (re-)established Danish research activity in biological oceanography. We focused on the opportunities generated by combining laboratory observations with field-based investigations; a combination that then and later has been fruitful for all members of the group.

When I started my work at DF&H in 1980, the size of the North Sea herring stock was at a very low level, and a fishing ban had been implemented. On that background, much

emphasis was on the herring and the possibilities of reestablishing a healthy North Sea stock. Consequently the spawning and early life of herring was our focus during the first years. Later, further attention was given to recruitment variability of the cod stock, and through time several of the important fishery stocks in Danish and Greenlandic waters have been in focus. Through time my research came to include larval fish communities from arctic, temperate, subtropical and tropical areas.

I have had the opportunity to keep a ‘red thread’ for a good part of my research, and it has – through quite many years – been my desire to assemble and combine the information from a series of key studies which have been published separately. In such assembly I wanted to emphasize commonalities and differences in the larval life of fish in a comparison across species and ecosystems, and synthesize the insight gained.

The project of writing the present thesis has been put off a long time, with many excuses for the delay. Excuses were often a wish to incorporate another, not yet finished, study in order to tell a story nicely rounded off. However, after a long life in science, I have to acknowledge that there is no such clean ending, and there will always be new discoveries and new questions around the next corner. Nevertheless, I’m glad that the latest work on eel larvae and their life in the Sargasso Sea could be part of the synthesis. This species and its oceanic larvae are so exceptional compared to species spawning in more coastal habitats, that it really challenges a synthesis of common traits among the lives of fish larvae.

I started writing the thesis in Danish, which was the tradition at that time. When the tradition changed, I decided to finalize the Danish version and subsequently translate the entire thesis. Thanks Bodil, for great help throughout. I’m grateful to an anonymous editor for checking the English spelling throughout. The English version is the official, submitted version, to which the Danish version is to be seen as a supplement.

I thank all who have contributed during the years, my colleagues with whom I have had splendid cooperation during the many research projects and those that have continued encouraging me to make this thesis a reality. Special thanks to Jan E. Beyer, Helge A. Thomsen and Torkel G. Nielsen for the many fruitful, enjoyable and hard-working hours we have spent together.

Resumé in English

Marine fish spawns thousands of small eggs and the hatched larvae becomes part of the plankton ecosystem of the open sea. The larva is a vulnerable stage in the life cycle of fishes and already during the initial fisheries research in the early 1900's it was realized that high and variable mortality in the fish larval stages is the cause of observed fluctuations in the fish stocks. Since this discovery it has been heavily debated to what extent life prospects of larvae depend on biological or physical constraints. However a wide range of interacting factors affects larval life and this should be perceived in a broader ecological context in which both bio-physical conditions and behavioral and evolutionary adaptations are taken into account. In this thesis I present studies providing insight into important life traits of larvae: their feeding, growth, mortality and dispersal/drift, and through cross-cutting comparisons between characteristics of species and their immediate environments I assess commonalities in larval adaptations and linkages between biology and physics. The findings point to a much more advanced behavior and ecological adaptability of larvae than generally believed. In spite of significant differences between investigated larval species in their morphology, development and experienced conditions there are obvious commonalities in their early lives. Strong linkages were apparent between fish larval life and physical characteristics of fronts and other marine interfaces, and observations point to a multitude of closely spaced habitats for fish larvae in the frontal zones. Thus the prospects of larval life, determined by the niche and the appropriate habitat, could be very species-specific and a likely variation in the overlap between niche and habitat would lead to variable mortality of larvae. Analysis of niche and habitat overlap could be a fruitful way to combine insights into biological and physical processes of importance in the fish larval life, and combined with cross-cutting comparisons this provides possibilities for marking out the dominating life-cycle processes of fish.

Resumé in Danish

Marine fisk gyder tusindvis af små æg, og de udklækkede larver bliver en del af havets plankton økosystem. Larve stadiet er af særlig betydning i fiskenes livscyklus, og allerede under den tidligste forskningsindsats i starten af 1900 tallet erkendte man, at de store svingninger i fiskebestandene havde baggrund i en høj og varierende dødelighed i larvestadiet. Det debatteres dog stadig, i hvor høj grad fiskelarvernes opvækst muligheder bestemmes af biologiske eller fysiske forhold. Der er en bred vifte af faktorer, der spiller sammen under larvernes opvækst, og vilkårene bør tydeligvis ses i en bredere økologisk sammenhæng, der inddrager både bio-fysiske, adfærdsmæssige og evolutionære aspekter. I denne afhandling præsenterer jeg en række studier, der behandler fundamentale karaktertræk ved larvernes fødeoptagelse, vækst dødelighed og spredning/drift, og gennem tværgående sammenligninger mellem arter og deres vilkår, ser jeg på fællestrækkene i larvernes tilpasninger og i samspillet mellem biologiske og fysiske forhold. Studierne viser at larvernes adfærd kan være langt mere avanceret og tilpasningsegnet, end hvad man generelt har antaget. Trods oplagte forskelle mellem larverne i deres morfologi, udvikling og vilkår, findes der også basale fællestræk. Der var en tydelig sammenhæng mellem fiskelarvernes opvækst og de fysiske karaktertræk ved fronter og lignende overgangszoner i havet, og observationerne peger på at frontzonen kan tilbyde mange, tætliggende habitat-muligheder for de forskellige arter af fiskelarver. Fiskelarvernes opvækstmuligheder, givet ved deres nicher og de mulige habitater, kan således være meget arts-specifikke, og ændringer i sammenfaldet mellem niche og habitat kan ændre larvernes overlevelsesmuligheder. Analyse af sammenfald mellem niche og habitat kan være udbytterig måde at kombinere vores forståelse for de biologiske og de fysiske processer der er af særlig betydning for fiskelarvernes liv, og i en kombination med tværgående sammenligninger vil metoden kunne styrke mulighederne for at afgrænse de vigtigste processer i fiskenes livscyklus.

Contents

1. INTRODUCTION

In this introductory chapter I will present a brief overview of the research into larval fish ecology (Section 1.1, partly based on the Introduction in Munk and Nielsen 2005), describe the hypotheses and concepts of special importance to my research (Section 1.2), and finally outline the objectives of the thesis and the overall methodology used across the primary studies (Section 1.3).

1.1 Historical context

Research into the life of fish larvae has a long history, and through time this research has made many important contributions to the fields of marine and fishery biology. Due to the great importance of fisheries to local communities, great emphasis has through the centuries been put on the fluctuations in size of fish stocks. Systematic studies of adult fish started in the early 1800's and investigations of early larval stages were initiated in the later part of that century. During those years extraordinarily large abundances of egg and larval stages of fish were found in many areas along the coast of European countries; for instance the Norwegian scientist G. O. Sars observed huge abundances of cod eggs in the Lofoten vicinity in 1888 (Sars 1889). Based on such observations scientists from countries around the North Sea started intensive research into the early development of fish, and during the late 1800's the basis of egg and larva identification and morphology was created. The Scotchmen J.T. Cunningham and E.W.L. Holt, and the Germans F. Heincke, V. Hensen and C. Apstein had great influence in this early pioneering work. The German scientist E. Ehrenbaum was exceptionally influential and productive. During the period 1894-1909 he published a series of important contributions, which have been central in the description and identification of European fish eggs and larvae during ensuing decades (e.g. Ehrenbaum 1897). A number of other researchers made important contributions during this period, and the period around 1900 was certainly the "golden age" of fish larva research. The spirit of this period appears in the introduction to Ehrenbaum's publication from 1897 where he writes: "*The interest in accurate information on the eggs and young stages of our fishes seems solely scientific, in so far as the purpose of our research is to distinguish and describe all developmental stages of animal life. However, when going further into this matter, it becomes evident that these studies provide numerous opportunities for dealing with and resolving practical questions of great importance.*" (my translation from German, as in Munk and Nielsen 2005).

At that time it was strongly debated whether the observed fluctuations in abundance of fish over the fishing banks were due to their migration to and from these areas, for instance whether apparent low abundances in the North Sea were due to fish migrating to the far north. The investigation of such “migration hypothesis” became a task for an international committee of scientists established under the International Council for Explorations of the Sea (ICES). This committee found that more knowledge was needed about spawning areas and the larval life of fish, and they encouraged an intensive and cooperative effort. A dedicated research program was subsequently carried out during the first decade of the twentieth century. The investigations included larger marine areas and more larval stages than hitherto had been covered and led to a series of new discoveries. During these investigations, two Danish scientists J. Schmidt and C.G.J. Petersen contributed important new knowledge about the early life of cod and flatfish, respectively (Schmidt 1905, Petersen 1909).

Marine scientists from the early 1900’s.

Participants at the 1904 ICES Statutory Meeting in Hamburg, German, here on board the RV "Poseidon”. Several of the mentioned scientists are probably to be found on this picture, but I have not been able to name individuals. Photo: ICES archive.

This international, collaborative research, led to the realization that the spawning of fish was much more restricted in time and space than hitherto believed. Based on the research and his own work on the age composition of herring and cod stocks, the Norwegian scientist J. Hjort presented a new theory in 1914, proposing a linkage between fluctuations in the fishery and variable recruitment of new offspring to the stocks. This theory was put forward in his famous essay on “Fluctuations in the great fisheries in the northern Europe” (Hjort, 1914). In the publication he also suggested that a specific “Critical Period” in the very young larval stages would determine the number of survivors from the spawning of a given year (the year class), those that would become a part of the stock. Following this interpretation by J. Hjort, larvae are sensitive to climate-related variations in feeding conditions during such critical period and consequently a temporal match would be necessary between food demands in the earliest stages and sufficient prey abundances. In the same publication Hjort outlined

another hypothesis, proposing that high mortality could be due to larvae being advected away from optimal nursery grounds. His work and theories were a great breakthrough in fishery science, but when underlining the key role of the larval stage in the stock size fluctuations, his work also led to a general change in the direction of research. Because of the assumed strong influence of climate on larval life and the following recruitment, J. Hjort and other scientists felt that continued research in these early stages would be of limited value. Instead, resources should be directed towards analysis of the age composition of the fish. This was based on the consideration that it would not be possible to foresee the current year class strength from the larval survival of any specific year. Instead age composition analysis of fish stocks should be used for estimating stock sizes and abundances of young fish recruiting to stocks and fishery.

A series of important research projects on fish larvae and their recruitment were, however, carried out during the following decades, but research on the early life stages of fish had lost its momentum. It was not until the mid-1960s that scientific focus was returned to fish eggs and larvae. This renewed interest in processes behind recruitment to fish stocks was stimulated by the "Aarhus Symposium" in 1970, which focused on stock development and recruitment variability (Parrish, ed. 1973). Two later symposia, in 1973 and 1979 on research on "The Early Life History of Fish," gave further momentum to the research in larval fish ecology (Blaxter, ed. 1974, Lasker and Sherman ed. 1981). The organizer of the first symposium, J.H.S. Blaxter contributed significantly to the research during subsequent decades, having already started before the symposia with a renowned review of "Development: eggs and larvae" in 1969 (Blaxter 1969).

Discussions of the causes of stock fluctuations and variable recruitment reopened during this new period of research on larval fish ecology, and new hypotheses were proposed based on the new understanding of fish' life cycles. A comprehensive list and description of these and later hypotheses have been given by A. Bakun (Bakun, 2010). Among the more important are: "Stable Ocean" (Lasker, 1981), focusing on the influence of strong turbulence which could disperse patches of prey important for first feeding of larvae, "Optimal Environmental Window" (Cury & Roy 1989), presuming that effects of wind and larger scale turbulence in upwelling areas might be critical and "Match Mismatch" (Cushing 1975), suggesting that there should be a temporal match between the emergence of fish larvae and their preferred prey. While these hypotheses are focused narrowly on the relationship between larvae and their prey, other hypotheses extend to the importance of hydrographic conditions and the dispersal and drift of eggs and larvae. Among these are the "Retention" (Iles and Sinclair 1982)," Member/Vagrant" (Sinclair 1988) and "Ocean Triad" (Bakun 1998) hypotheses. The reasoning behind the retention and member/vagrant hypotheses has been of great inspiration for my research and these will be treated in more detail in the following section.

During the last twenty years, research related to the life of fish larvae has broadened, and publications on this topic have increased substantially in number. Recent reviews on larval feeding (Nunn et al. 2012), growth (Llopiz 2013) and dispersal (Leis et al. 2013) illustrate the extent of information now available for numerous of larval fish species. Thus there is much activity in this field of research, which is positioned at the intersection of a series of classical research disciplines, including aquaculture research, fisheries dynamics, plankton ecology and biological oceanography.

1.2 Central hypotheses and concepts

During my work I have been inspired by a series of hypotheses, concepts and analytical models that I have found valuable for the interpretation of biological/physical information of relevance to larval fish ecology. Some relate to specific processes of larval feeding and growth and will be considered together with those in subsequent sections; here I will briefly outline the two influential hypotheses on retention areas and life cycle closure of fish, and introduce the niche concept as a vehicle for furthering the interpretation of bio-physical linkages during the early life of fish.

The Retention Hypothesis

The physical/spatial aspects of marine habitats and their importance to life of larval fish are central in the pioneering works of T.D. Iles and M. Sinclair in the 1980s. Their original formulation of the retention hypothesis was based on the observed relationships between the extents of distinctive geographic features and the sizes of the herring stocks spawning in those specific areas (Iles and Sinclair 1982). They proposed that distributions of larvae from given stocks are delimited by hydrographic processes and that tidally induced front formation creates barriers to larval drift. Areas with natural physical barriers, for instance fjords, are included in this interpretation of retention. According to the hypothesis maintenance of fish stocks requires hydrographically stable areas for their early life, areas which minimize dispersion and drift of eggs and larvae. The limit of a stock's size would be set by the capacity of its nursery area [1] and determined by its spatial extent and level of productivity. Early stages find lower capacity of the nursery areas than experienced by the later stages, and as a consequence these physical/biological relationships during the early stages could be seen as a bottleneck in the life cycle of fish.

[1] Here the term 'nursery area' appears for the first time, and a comment on the use will be appropriate. A 'nursery area' is mostly used to describe the area of distribution, feeding and growth for the later larval and juvenile stages. I find the term suitable when defining these areas for all feeding larval stages, and will use it accordingly.

This proposal challenged the prevailing assumption that the large year-to-year differences in larval survival and recruitment were due to variations of the temporal overlap between emergence of larvae and their prey. This was assumed in the above mentioned critical period and mismatch hypotheses (Hjort 1914, Cushing 1975). The retention hypothesis also opposes other hypotheses that only focus on the drift of eggs and larvae, on their ability to "make their way" from spawning areas to nursery areas. As pointed out in later works by M. Sinclair there will be a fundamental difference between interpreting currents and dispersion as something positive for the population (providing larvae opportunity to reach adult foraging areas), and the interpretation of the retention hypothesis that dispersion and drift are undesirable in an evolutionary context. The supposition is that these should be minimized in order to keep eggs and larvae within a delimited, suitable area and hence, that the adults will migrate to sites for spawning where this is achievable (Sinclair, 1988).

Member/Vagrant Hypothesis

In his essay "Marine population" M. Sinclair extended the concept of retention areas to a more general hypothesis covering evolutionary aspects for all marine populations with pelagic juvenile stages (Sinclair 1988). The basis of this hypothesis is a selection against the free crossing of individuals, when there would be an evolutionary advantage of restricting mating to members of a group which meets at a specific mating locality and time. This process results in creation of species and to distinctive populations within species. Free crossing can be minimized when populations are kept within restricted geographic areas where they will be well adapted to fulfill their lifecycles. Consequently these must be areas where membership surpasses vagrancy. On the basis of this hypothesis M. Sinclair explained a series of observations on the distribution and abundances of marine populations, especially by examples from herring populations. He explained the pattern and richness (the number of distinctive populations within a given species) as a function of the number and location of geographic settings within which the lifecycle of the species is capable of closure, while the absolute abundances of the populations are scaled to the sizes of the suitable geographic settings. As in the retention hypothesis, it is inherent in the member/vagrant hypothesis that processes in the pelagic/larval stages are to be seen as a bottleneck in the lifecycle of fish, while the area of distribution in these stages is more restricted and sensitive than that of the later stages. The nursery areas are influenced by both short- and long-term changes in oceanographic conditions, which consequently would be the most important cause for the observed fluctuations in the recruitment.

In his 1988 essay M. Sinclair distinguished sharply between energetic processes, which lead to selection and adaptation in the food chain, and spatial processes (mainly physi-

cal) that restrict free genetic crossing and lead to population-size regulation and lifecycle selection. That distinction might be relevant in order to emphasize the ultimate importance of closing the lifecycle in a spatial context, but it tends to ignore the important spatial aspects of the energetic (food chain) processes. All processes of importance to the larval life take place and interact in a three-dimensional physical space, and the full multitude of biological and physical processes and their interplay ought to be considered when interpreting the larval life as part of the full life cycle of fish.

The niche concept

The niche concept affords the possibility to view both biological and physical/chemical processes within the same theoretical frame. The concept has been of fundamental importance in ecological research and theory development; basically, the notion of niches expresses the environmental dependence of the organism and its influence on the environment. Through time the concept has been much debated. Chase and Leibold (2003) present a historical review of this discussion and illustrate how different definitions of the niche have shifted in popularity. A simple, still widely used definition was presented by G. E. Hutchinson in 1957. He introduces the niche as an "n-dimensional hypervolume in which each point defines the environment providing a species the possibility to exist indefinitely". Each dimension describes the relationship of the organism in respect to a specified environmental factor, and resources appear distinct from other limiting factors of the environment such as physical factors (Leibold 1995). These factors describe the *fundamental niche*, which under influence from predators and competitors would be further limited to the *realized niche* (Hutchinson 1957). Decisive to existence and abundance of a species would be the overlap between its niche and a geographical habitat that satisfies that niche. In this context there is a distinction between conditions providing the species opportunities to 'exist indefinitely', i.e., surroundings that in the long perspective satisfy all fundamental niche demands for all stages in the life cycle, and conditions that satisfy the niche demands of a given stage 'here and now'. Niche width, physical dispersal, and the availability and stability of the habitat are all important components of the relationship between niche and the distribution of an organism (Pulliam 2000).

An understanding of niche demands and the overlap between niche and habitat could be used in a broader interpretation of "retention areas" and "member/vagrant's". The key proposal of the hypotheses, that larval populations should remain spatially restricted, could be seen as a demand for finding sufficient habitat of low-dispersive character. The need for diminishing the dispersal of larvae would thus be only one, however very important, component of the full niche, and a range of other demands will further

restrict the useable habitat. I will return to these considerations in an interpretation of present findings in section 6.2.

1.3 Objectives and Methods

Objectives

The ideas of the fish larval life being restricted by, but also to some extent being adaptable to, specific biological and physical constraints, have been central to the research presented in this thesis. Focus has been on developing comparable information on the fundamental aspects of larval life: their feeding, growth, and retention/drift, using a broader ecological approach to distinguish key processes and linkages.

By analyzing important environmental characteristics and larval adaptations in comparisons that extend across scales, stages, species and ecosystems I have searched for commonalities and differences. Thus, much weight has been given to the comparative approach. This is more or less apparent in the primary publications, but in this thesis I draw further on the possibilities for interpretation and comparison. The notion has been that with further insight into commonalities and differences among lives of fish larvae we will be able to distinguish processes of universal importance to fish reproduction, larval recruitment and life cycle closure.

Thus, the overall objective of the present thesis has been to extract the key aspects of larval fish ecology based on a series of comparable research studies, focusing on common characteristics and adaptations, on insight gained from cross-cutting comparisons and on an evaluation of niche demands and habitat restrictions.

Methods

The methods of the primary studies included both laboratory based experiments and field based sampling during long distance cruises. Accordingly the studies covered a wide range of scales, where the relevant scale changed depending upon whether my focus was on the individual, group or population (Fig. 1). Scales ranged from centime ters to kilometers, and the smaller scales were seen as embedded in the larger. The broad coverage of scales in observations and sampling provided valuable opportunities for combining and analyzing information across scale. I will return to the scale aspects in Section 6.1

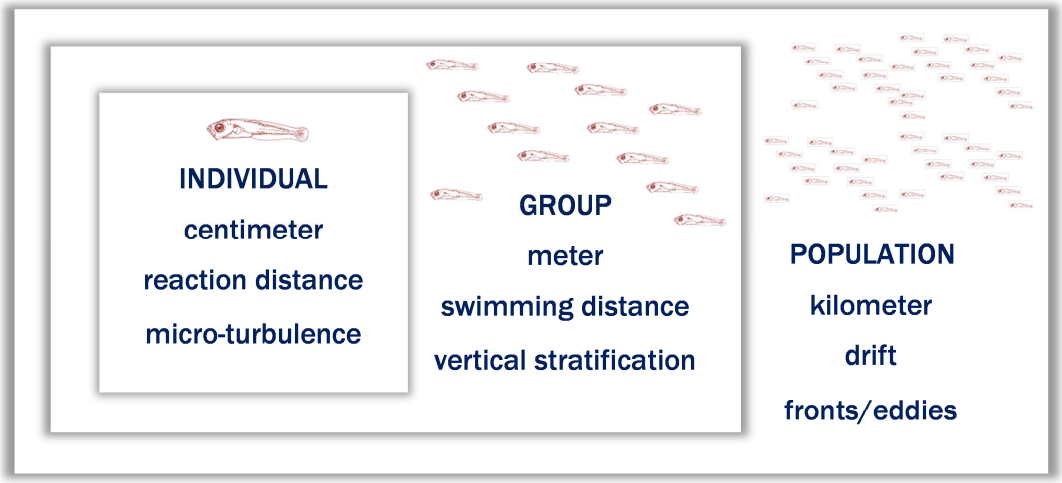


Figure 1. Schematic illustration of important spatial scales in the life of fish larvae

The smallest scale primarily covers larval reactions to the immediate environment, influenced by micro-turbulence. The intermediate scale covers distances within reach by active swimming, mainly relevant for the vertical migrations in the stratified water column. On the large scale processes of importance to the population take place, larvae disperse and drift and are influenced by characteristic physical features such as fronts and eddies. The small scale is imbedded in the intermediate, which is embedded in the largest.

In the laboratory the same standardized rearing tanks and experimental setup were used throughout. Larval behavior was registered by visual and video observations while growth was measured from larval sampling in the rearing tanks. Both for registration of behavior and of growth, we used cohorts of their natural prey organisms for feeding. These cohorts were obtained by culturing adults of different copepod species and raising daily batches of copepod eggs to specific stages. Further emphasis was put into keeping a constant, homogeneous prey environment for larvae by injecting standardized turbulence to the tank and by frequent control of prey densities.

During field cruises we prioritized consistency in our use of methods. Standardized sampling sequences were often used at given positions (stations) ensuring concurrent relevant physical/chemical measures (by CTD casts through the water column), and a consistent sampling of plankton organisms at all trophic levels. Mostly, information about both plankton abundances and of relevant rates were obtained. Algal abundance was measured by their fluorescence, calibrated to chlorophyll *a* content. Zooplankton were sampled by either submersible pumps or standard nets, and fish larvae were sampled by the same ring-net gear (however, mesh sizes could differ). Productivity of algae was measured by C_{14} methods, copepod productivity measured by the egg

production of adult females, and growth rates of larvae were later estimated from their size and an otolith based ageing. In addition to the standard sampling, vertically stratified sampling was often carried out at specific sites. A wide array of valuable additional information was gained from other gears; among those were current measures from an Acoustic Doppler Current Profiler, acoustic backscattering from an echo sounder, and surface temperature from satellites.

The emphasis on standardized methods and sampling schemes provided us with good opportunities for comparing across species, sites and seasons. Thus such "comparative approach" has been important for the further interpretations of "single" results. The comparative methods have a long tradition in biological research, for example in the systematic investigations of species in the early 1900's, and these methods still provide great opportunities for fisheries research, specifically the research on recruitment to the stocks (Bakun 1985, 2010). With all the possible interacting factors affecting the larval life, a simple, significant relationship is just not likely. The comparative approach, in which the search for similarities and differences progressively marks out the dominating processes and mechanisms, is a much stronger tool in the quest for generalities (Bakun 2010).

My presentations and comparisons will cover the fundamental aspects of larval life: its feeding, growth and survival, and they will – with reference to the hypotheses and concepts described in section 1.2 – put additional emphasis on the spatial aspects of larval fish ecology - the adaptations and the biophysical linkages. Thus, the following presentations are organized in these chapters: 2. 'Prey search', 3. 'Prey availability', 4. 'Growth and mortality' and 5. 'Spawning and nursery areas' (in here the larval distribution and drift).

Each chapter is based on information from the primary publications, and a specific reference to one of these is indicated by a number in squared brackets e.g. [4]. The digit refers to a number given to each of the primary publications, apparent in the list of publications at the end of the thesis and at the front-page of each of the included publications. Most figures are prepared specifically for this thesis emphasizing comparisons between studies and using data from the primary publications. The figures and photos are to be seen as supplements to the text and have extended legends. They are briefly referred to in the text, but are not as such linked to the text.

2. PREY SEARCH

Searching for prey and prey consumption are basic activities for all animals. These activities are necessary for the single individual, but they also basic for the functioning of the entire ecosystem. Consequently prey-predator relationships have been intensively studied, and a rich literature is available on prey searching by fish larvae, analyzing the basic interactions between prey and predator.

A major challenge to the fish larva as predator is the significant heterogeneity in the prey environment. Feeding conditions change both in space and time, and a behavior suitable in one set of conditions will be inadequate in another setting (Dill 1983). Hence, we would expect that fish larvae are capable of varied modes of prey search in the constantly changing prey field. They should be able to respond to the changes, and their behavior should have the plasticity necessary for suitable adaptation to the new circumstances.

This expectation of a well-adapted and flexible behavior of fish larvae has been central to my research into prey search by fish larvae described in the following sections. First I will investigate components of larval prey search to uniform prey (Sections 2.1-2.2 based on [1, 9]), then consider reactions to prey of different size (Section 2.3 based on [6]), look into the influence from light and turbulence (Section 2.4) and finally ascertain the prey search involved in larval vertical migrations (Section 2.5 based on [4, 21]).

2.1. Prey densities, activity and efficiency

When analyzing larval reactions to prey, their behavior can be divided into a series of components, inferred according to the so-called disc-equation (Holling 1959). A predator like a fish larva using vision for prey discovery will react to prey within a certain area given by the swimming speed of the predator and the distance at which a given prey is visible. The reaction within this area will depend on the prey density (D). Before discovery of the prey leads to its consumption, the predator has to chase, attack and finally catch the prey. Each of the components in the prey search is influenced by a series of factors and each of these takes up a part of the available time for prey search. Beside this, the predator will have to digest the prey. As consequence it cannot consume prey indefinitely, and its functional response, which expresses the change in prey intake at changing prey densities, will approach a plateau at the higher prey densities.

These relationships are described by the disc equation, which Real (1977) expresses by:

$$A = (MA*D)/(HD+D) \quad \text{Eq. 1}$$

Here A expresses the rate of search, determined by one of the events in the sequence during the search: the hunt, the attack or the consumption; MA is the maximal search rate, and HD is the density at which the search rate is half of MA.

The efficiency of a predator in relation to the event sequence of the prey search can be expressed by the rate of reaction (C) in a given area. To fish larvae this "area" will be a volume (D), and for the number of reactions (R) which lead to an attack (R_a) over time (T, which does not include time spent in the attack) this efficiency is expressed by:

$$C_a = R_a/ (T*D) \quad \text{Eq. 2}$$

If a measure of attack success (AS) is available this can be considered in calculating what is often named clearance as $C_f = C_a*AS$. Eq. 3

Using a set of assumptions we can estimate the physical distances involved in prey search. At low prey densities, when search rate would be close to the maximal MA, C will express the search in a physical volume given by the area of a circle around the head of the fish larva times its swimming speed SS. Search might however, not take place in the full circle, hence we define a form factor (FF) expressing the part of the circle that is searched. For reaction leading to attack with the efficiency C_a we can express the distance of reaction MDR:

$$MDR= (C_a/ (FF* \pi *SS))^{0.5} \quad \text{Eq. 4}$$

These considerations about predator behavior are the basis of the analyses of prey search behavior of larval herring (*Clupea harengus*) and cod (*Gadus morhua*) [1, 9]. Here we investigated larval behavior across a range of prey densities. We put priority on the use of natural prey organisms (nauplii of the copepod *Acartia tonsa*) of consistent size and in densities commonly found at sea.

The larvae were used 2 to 3 weeks after hatching, and their behavior was registered by direct, visual observations in experimental tanks set up at a range of different prey densities. Both herring and cod larvae showed a functional response where the rate of attack rose toward a plateau at increasing prey densities (Type 2 response, Holling 1959) (Fig. 2). In exhibiting this functional response, both species showed significant behavioral changes, which were especially apparent when the prey density dropped below 30 liter^{-1}. The duration of prey handling was very short and was not related to prey density, hence most of the changes appeared in larval search rate (A) and the time used for prey search (T).

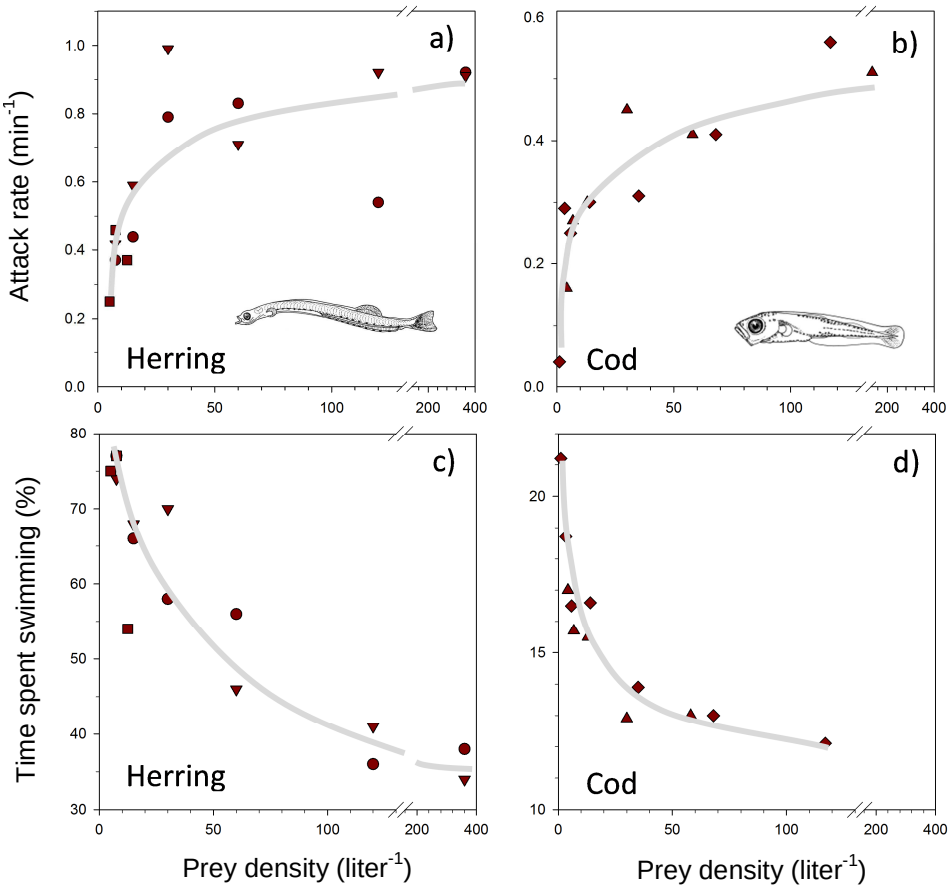


Figure 2. Fish larval reaction to changing prey density

Prey search of herring and cod larvae related to density of *Acartia tonsa* nauplii. a) - b) Attack rate increasing at increasing prey density, levelling off at the higher densities. c) - d) Swimming activity declining at increasing prey density. An immediate, large change was seen at the lower densities, levelling off at the higher values. Absolute differences between herring and cod larvae were due to differences in swimming modes and registration of activity. From [1, 9].

Certain elements in the mode of larval swimming are central for the understanding of the observed behavioral changes and adaptations. The long, slender herring larvae show varied swimming modes, shifting between undulating movements of their relatively long bodies and more abrupt movements of shorter duration (Rosenthal 1969). Cod larvae, on the other hand, have a different body shape (Fig. 2) and they use only abrupt swimming bursts of short duration (0.2 sec.). Often the herring and cod's larval swimming modes are used as examples of two characteristic types of swimming: the cruising and the pause-travel. For both species we found increased activity at the lower prey densities (Fig. 2), and it appears that the activity change differs between the two modes

of swimming. For herring larvae we registered a significant increase in the duration of swimming movements, and at very low prey densities the long-lasting undulating movements took up to more than half of the total active time. For cod larvae the increase in the duration of swimming events was marginal, while the frequency of the events rose markedly. Further, the time spent by cod larvae in pauses between the swimming bursts drops at the lower prey densities. Conclusively, when the intensity of search increases for the species, the herring mainly respond by increasing the duration of searching in undulating swimming events, while the cod larvae carry out increased numbers of short forward, searching moves.

The intensified prey search is also evident from a calculation of the effectively searched volume ('clearance') based on the registered rate of attack (C_a) at different prey densities. Here the success of attack is included, being independent of the prey densities (Kiørboe & Munk 1986). The volume that was effectively searched per minute rose from 0.1-0.2 liter at prey densities 100 liter^{-1} to 1.1 liter (cod) or 1.6 liter (herring) at the lowest densities investigated. This huge increase in effectively searched area is, however, not only due to the increase in swimming activity. This became evident when we calculated the distance to prey recognition, based on Eq.4. For both species we found that this distance of reaction dropped markedly at greater prey density. While the distance of perception is independent of prey density this shows that the willingness to react increases when prey density decreases. At the very low prey densities, we expect that the majority of prey perceptions will lead to a chase and an attack attempt, hence in those cases the distance of reaction will approach the distance of perception (for this type of prey in the experimental circumstances). The largest average distance of reaction, which then is assumed to equal the average perceptive distance, was approximately one body length for both herring and cod larvae: 1.5 and 1.1 cm, respectively.

The increased search rate at declining prey densities implies that estimates of larval capability for prey consumption based only on observations made at high prey densities are misleading. While fish larvae are often reared in very high densities of prey, and often with irrelevant prey organisms, such as the anostracan *Artemia salina*; observations in such rearing conditions could easily underestimate larval skillfulness and adaptability.

The intensified search by larvae in order to sustain good prey consumption rates in low prey densities, will increase their metabolic costs. So, what is the balance between intake and expenses? Using the same experimental setup as in [1], Kiørboe and Munk (1986) investigated the balance for herring larvae. We estimated that increased activity due to the change from the highest to the lowest prey densities (from 35% to 90% time spent swimming) potentially would result in a 33% extra weight loss (per unit time).

However, that is counterbalanced by 50% improvement of prey search to attack, and hence consumption, from this increase in activity [1]. We found that the herring larvae satisfied their basic needs (i.e. zero growth) at the lowest prey experimental prey densities of about 10 liter $^{-1}$, obtained a specific growth rate of 3% d^{-1} at 30 liter^{-1} and reached the maximal growth rate of 7% d^{-1} at densities above 100 liter^{-1} (Kiørboe & Munk 1986). The cod larvae used in the behavior experiments [9] showed a maximal growth rate of 8% d^{-1}, a rate which was obtained at prey densities as low as 30 liter^{-1} (P. Munk. unpubl. results).

2.2 Reaction time and hunger.

In the investigations presented above the larvae experienced their experimental prey densities during an extended period of several days. Hence, in that setup the response in search velocity was not immediate, but it developed gradually under constant prey conditions. In order to evaluate larval capability to quickly respond to changes, I used a setup where activity of cod larvae which had experienced an abrupt decline in prey density was observed [9]. The objective of these experiments was to estimate the speed at which larvae are able to change behavior, and to evaluate whether search behavior is

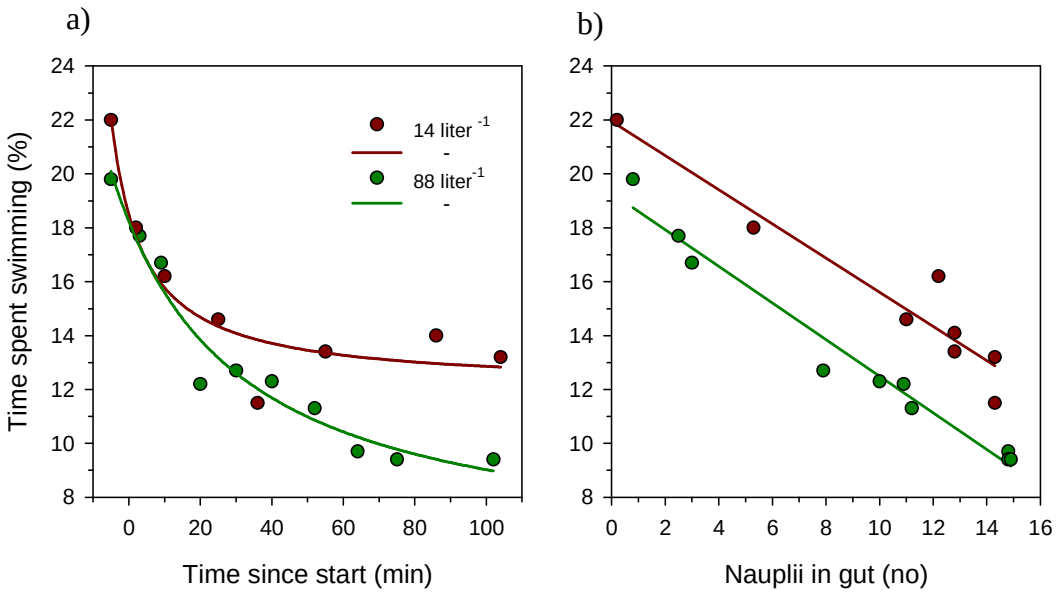


Figure 3 Behavioral changes of cod larvae due to hunger and perception of prey

Larval activity was registered by the time larvae spent swimming and related to prey consumption. a) After larvae being fed at time zero, their activity declined during time when more and more prey became consumed. Activity reached different levels dependent on prey density indicating an influence from density per se. b) Activity was higher at lower levels of satiation, measured by copepod nauplii in the gut. At same satiation levels, larvae were slightly more active at the lower prey density than at the higher. From [9].

guided by sense of hunger or by cognitive registration of the prey density. The initial prey density was zero, and larvae had experienced that during at least 12 hours in two experimental series. Prey densities in those experiments were then raised to 14 and 88 prey liter^{-1}, respectively, and the activity was registered during the following 100 min (Fig. 3a). Within the first few minutes larval activity declined markedly from an initial level of 20% of time spent swimming (activity), and after half an hour the activity had dropped to the level observed earlier at constant prey densities of the same magnitudes (14 liter^{-1}: ~13% activity; 88 liter^{-1}: ~11% activity).

We expect the sense of hunger and satiation in the larvae would be mediated by the physical influence of contents on the stomach and gut and by the digestion products transferred to the blood. The cod larvae sampled in the experiment described above were analyzed for their gut contents, and the registered activity was related to the numbers of prey nauplii in their gut at the time of activity estimation (Fig. 3b). Larval activity showed a linear decline with increasing gut contents, and moreover the relation between stomach content and activity differed between the two prey densities used in the experiments. Hence, both the gut content and the prey density in the habitat appeared to influence larval activity, indicating that larval behavior is directed by several stimuli.

2.3 Prey size and predator/prey relationship.

The experiments described above used relatively similar prey organisms, i.e. uniform cohorts of the same prey organism (*Acartia tonsa* nauplii), to eliminate effects from prey size and type differences when investigating the effects of prey density and hunger. In this section I will examine prey size effects.

The searching of predators among prey of varied types and sizes has been investigated and described in a series of hypotheses and models, of which several basic theories were introduced by the 1970s. The more influential ones have concerned “Visible Prey Size” (VP) and “Optimal Foraging” (OF). In VP it is assumed that the reaction of the predator is related to how large the prey appears in the field of vision (O’Brien et al. 1976). In OF the emphasis is on the adaptations of the predators for maximizing the energy gain from prey search (Schoener 1971, Pyke et al. 1977); it is implied that increased prey intake leads to better survival and enhanced possibility to reproduce and hence that there would be a direct evolutionary advantage to simple maximization of the intake.

Neither the VP nor the OF afford a complete coverage of the processes, but because of its simplicity the VP has been applicable to basic analysis of predator behavior. A larger

prey will be more visible than a smaller one, and if two prey organisms were at same density the predator would be more reactive to the larger than to the smaller. On the other hand, the success of attack would decline because the larger the prey would have a better escape response than the smaller. Thus, larval feeding as function of prey size can be expected to take a dome-shaped curve, where ingestion increases gradually due to increasing visibility of the prey, and then declines after reaching a maximum due to the increasing difficulties in catching the prey.

When investigating the general aspects of predator behavior and consumption in relation to prey size, the simple linear scale has certain limitations. From linear measures only we cannot do proper comparisons across stages and species. A relative scale where processes and consumption are expressed by size-ratios between predator and prey would be a much better analytical tool for evaluation of prey availability. Hence, in my investigations on the importance of prey size to larval feeding, I have put much focus on relative prey/predator size scales.

To examine whether larval search behavior could be expressed on a relative prey/predator scale, I set up experiments with a series of combinations of larva and copepod sizes [6]. These investigations covered a broad size spectrum of both larvae (13.5-44.8 mm) and copepods (0.1-2.2 mm), and this provided the possibility of examining a series of (overlapping) combinations of relative sizes. Measurements of attack rates and attack success were based on systematic, direct observations in the tanks using the same methods as for investigations of variations in prey density [1, 9].

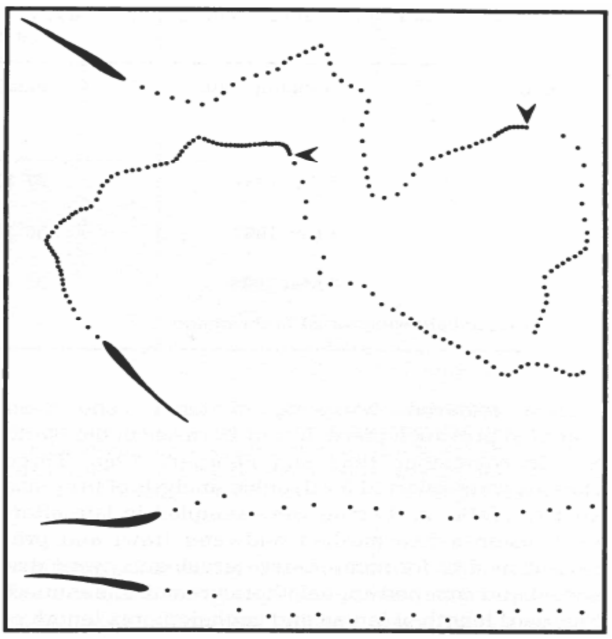


Figure 4. Swimming modes of herring larvae at different prey availabilities.

Larvae are viewed from above, each dot show larval position every 0.04 second, arrows point to onset of prey attacks. The two upper larvae experience an environment with attractive prey, and they frequently change speed and direction. The two lower larvae do not meet prey of attractive size and swim fast in the same direction. From [6].

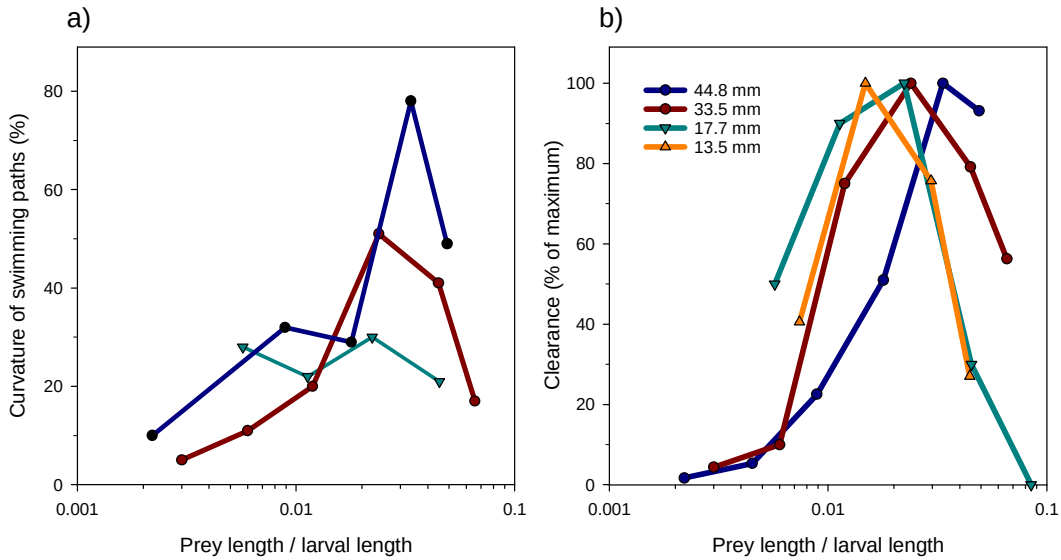


Figure 5. Larval behavior as function of the relative prey size in the environment.

Behavior of different length groups of herring larvae reared at a range of copepod sizes are compared on a relative prey size (log-scaled) axis. a) Curvature of swimming paths increases with relative prey size to a maxima at about 0.03, and levels off at larger prey sizes. Paths as illustrated in Figure 4. b) Relative magnitude of clearance (effectively searched volume) approximating modal distributions on the log-scaled relative prey size, maxima were seen at about 0.02-0.03. From [6].

However, here the analysis of swimming behavior was based on video recordings by a camera mounted above the tanks [6]. Swimming speed was estimated from estimates of length of swimming paths, time to transit them and their curvature, expressed as the actual length of swimming path divided by distance from start to end (Fig. 4).

The investigation showed a significant change in larval behavior as a function of relative changes in prey size. At greater prey sizes the larvae lowered their swimming speed, and they changed direction more frequently. The curvature of swimming paths was maximal at relative prey sizes of .03 to .04 (Fig. 5a). Larval reactions toward prey and the attack success showed common traits, these best revealed on a relative prey-size/predator-size scale. The efficiency of search expressed by C_f (see Eq. 3) was calculated on the basis of the measured attack and success rates at the different combinations, and an increase toward a maximum followed by a decline was seen for all four size groups of larvae (Fig. 5b). The distances of reaction (Eq. 4) showed a strong increase as function of the relative prey size. This illustrates the importance of the greater visibility of larger prey, and while the swimming speed toward larger prey items declined, the increase in distance of reaction appeared as the major cause of the efficiency increase. The reason for the subsequent decay in efficiency is apparent from a

strong decline in attack success when prey gets even larger; they get better at escaping. In conclusion, to a good approximation the search efficiency of fish larvae can be described by a bell-shaped curve over a scale expressing the relative sizes of prey.

2.4 Influence of light and turbulence.

The observations of prey searching by fish larvae [1, 6, 9] were carried out using constant physical conditions. Two physical parameters are of special significance to larval search for prey and influence experimental and field observations. These are the light intensity and the turbulence of the water. Light intensity influences the perception of prey and thereby the probability of a larva finding prey, while turbulence influences the relative movement between larva and prey and thus both the larva's encounter rate and its ability to chase prey.

Light intensity

Search for prey does not take place until the light intensity passes a visual threshold. That is on the order of 0.02 $\mu E\ m^{-2}\ s^{-1}$ for e.g. herring and cod larvae (Batty1987, Ellertsen et al. 1980). At light intensity above that lower limit, the larval field of perception increases significantly, but it reaches a level at which further increase has little influence on the field of perception. That level is reached at 10-20 $\mu E\ m^{-2}\ s^{-1}$ (Batty1987, Fiksen et al. 1998). The experiments in [1, 6, 9] were carried out at 23 $\mu E\ m^{-2}\ s^{-1}$ at the surface and approx. 20 $\mu E\ m^{-2}\ s^{-1}$ at the observation depth of 0.5m. Accordingly we have observed larval feeding behavior at a light intensity sufficient to sustain maximum perceptual ability, and at which we would expect marginal influence from slight changes in light intensity.

Because of the strong attenuation of light in water, the field of perception in water is much shorter than in air. Additionally, the amount of particles in the water (its turbidity) may further attenuate the penetration of light. Fiksen et al. (1998) illustrated by models on feeding of herring and cod larvae how relatively minor increases in transparency of water have strong impacts on the larval field of perception and on changes of that field down the water column. Another relationship, pointed out by Giske et al. (1994), is that the influence of light intensity on feeding abilities changes down the water column, depending on the size and contrast of the prey. They found that the relative influence of light on the perception distance increases down the water column, though this influence is less important for the more visible prey, i.e. those larger and with greater contrast. Hence, light intensity and water transparency are important determinants of the vertical distribution and migrations of plankton. This will be considered further in Section 2.5.

Turbulence

Wind, waves, currents and tidal excursions generate turbulence. At large scales (meters) turbulence influences the structure of the water column and the distribution and dispersal of plankton, on very small scales (cm) turbulence might influence the contact rate between plankton organisms.

An increased contact rate due to increased turbulence might improve the possibilities of fish larvae to detect their prey. This has been illustrated experimentally (MacKenzie and Kiørboe 1995) and appears from results of field observations (Sundby and Fossum 1990). There might however be a downside to turbulence. Strong turbulence might disturb the larvae in their pursuit and attack of prey. MacKenzie et al. (1994) analyzed this aspect and found that the ability to approach prey and reach a good position for attack is affected. Attack success, once larvae have positioned themselves close to the prey and are ready for attack, would be less sensitive.

The impact of turbulence might also be the basis of the often observed discrepancy between the functional responses determined in experiments and the consumption rates in the field determined from either stomach contents or growth rates (MacKenzie et al., 1994). Rearing experiments are often carried out in quite stagnant water with slight or no turbulence, and the positive influence of turbulence is not operative. To avoid that effect, we induced turbulence in a standardized way in the rearing tanks for our experiments [1, 9]. Our results for feeding ability stand out as being in much better agreement with observations of feeding and growth in the field ([9], Kiørboe and Munk 1986).

2.5. Prey search and vertical migrations

Prey density, light and turbulence vary considerably in the water column, and fish larvae have the opportunity through vertical migrations to pursue conditions that provide the best food intake and growth. As described above, fish larvae change behavior as a function of food intake; at greater intake they lower their swimming speed, and they change their direction of swimming more frequently. This reaction could influence vertical migration while the time spent in an area offering good feeding possibilities would be longer than in a less attractive area. Hence this might be one of the mechanisms determining vertical distribution of fish larvae.

In a field investigation of vertical distribution and migration [4], we examined the relationships between distributions of herring larvae, light and prey conditions down the water column. This investigation took place in the North Sea and was divided into three periods extending from hatching to a larval age of approx. 3 months. In October the prey (copepods of several species) were concentrated at the pycnocline at 40 m depth,

and at noon we also found the herring larvae at this depth. At dawn and dusk larvae migrated to the upper 10 m. During September and November the copepods were relatively homogeneously distributed in the water column, and then the larvae remained in the upper 10 to 20 m throughout daylight. During all periods, the larvae were positioned deeper during night than during day. During the vertical migrations, the concentration of larvae changed. This was illustrated by the variation in Lloyds patchiness index which expresses how concentrated larvae are in certain strata (Lloyd, 1967),. Conspicuous concentration at depth was seen around noon, when the light intensity was peaking.

The findings suggest that the vertical migration of fish larvae to a large extent would be directed by their feeding opportunities: Larvae migrate to depths determined as a compromise between obtaining best possible light conditions and best possible prey density. However, neither the interpretation of “best light intensity” nor of “best prey density” is straightforward. There is an interplay among a wide range of physical and biological effects including water transparency, water density, turbulence and prey characteristics.

It is commonly observed that vertical distributions of different species of fish larvae differ in the same water column. Thus, not all species of larvae migrate to depths where a maximal density of copepods is found. It appears that migration could be directed by species-specific prey preferences (prey sizes, species). Such influence was illustrated in a comparative investigation of five species of gadoid fish, an examination of the respective vertical and horizontal distributions of their larvae. We sought likely causes for the differences [21]. The investigation was carried out in Skagerrak, where larvae of whiting (*Merlangius merlangus*), cod, haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*) and Norway pout (*Trisopterus esmarkii*) had overlapping distributions within a relatively limited area at a hydrographic front. Both the vertical distributions of larvae and of their potential prey followed the depth of the pycnocline, hence distributions were shallow when the pycnocline was shallow and visa versa. In general, the average depths of distributions varied from 30 to 60 m. Each species of both fish larvae and copepods had a characteristic depth position relative to the other species of their taxonomic group (Fig. 6) and it appeared that a given larval species and its preferred prey followed each other across the area. Hence, the findings indicate a form of vertical niche differentiation, in which larvae of each species find position among its preferred prey.

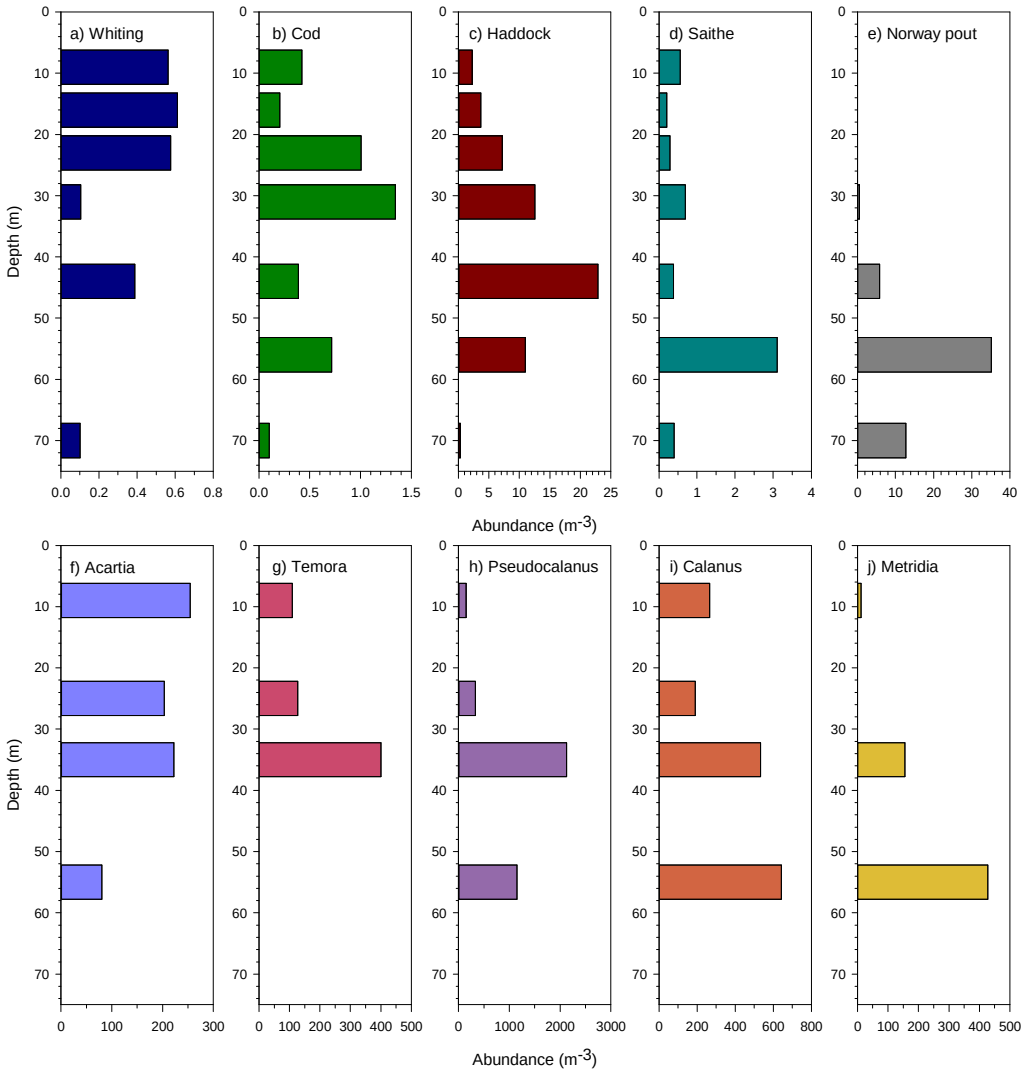


Figure 6. Vertical distributions of fish larvae and copepods in a frontal area.

a)– e) Five species of gadoid fish larvae. Sampled by opening-closing gear (Bioness) in the given depth strata of the same water column. Distributional patterns differed, with species-specific average depths of distribution.

f) - j) Five genera/species of common copepods sampled by submersible pump. Are potential prey items for the larvae sampled in the vicinity of this sampling site. As for larvae the findings indicate species-specific distributions. From [21].

As mentioned, the degree of turbulence might impact the pursuit of prey by fish larvae, and that might shape vertical distributions. Wind-induced turbulence is strongest at the water surface and diminishes downward, while tide-induced turbulence is strongest at the bottom and diminishes upward (Simpson et al, 1990). Consequently, there will be a

gradient of turbulence through the water column, which will vary under the influence of wind and the tidal cycle. Our first investigation of the vertical distributions of herring larvae [4] was followed by a more extensive investigation, specifically aimed at estimating the relative importance of light variation and wind- and/or tide-induced turbulence (Heath et al. 1991). In this we completed 10 collection series and used the longest to analyze the correlation between changes in the physical relations and the pattern of larval migration. The analysis showed a distinct 24 hour cycle in the migrations and the larval concentrations equivalent to what we found earlier [4], but there was also an indication of influence from wind and tide. Larvae were concentrated at shallower depths during flood tides and migrated deeper when there was a strong effect of wind. A connection between vertical migrations and the tidal cycle is seen also in other investigations in coastal areas. These migrations are hypothesized to afford possibilities to minimize dispersion and drift (e.g. Fortier and Leggett 1983).

Depth stratified sampling with opening-closing nets.

This photo shows the retrieval of the common Multinet, in a version of 0.25 m^2 opening and 5 opening-closing nets. This gear is developed mainly for stratified sampling of plankton smaller and more abundant than fish larvae, but is applicable for larvae in their very early stages. For the vertically stratified sampling of larger fish larvae, described in the studies [8], and [21], we used a 1 m^2 Bioness, which is heavier, more complicated and less reliable (!). The stratified sampling in [4] was based on simple ring nets, sequentially sampling in a series of depth strata. Photo: P.Munk

3 PREY AVAILABILITY

Availability of appropriate food organisms is fundamental to larval feeding and growth. The investigations of larval feeding behavior in Chapter 2 showed the great flexibility of fish larvae in their response to changes in feeding conditions, and how a series of behavioral and physical characteristics influence their consumption of prey. This influence is expressed by the prey preference, which can be studied in the field by comparing actual consumption to prey abundance in the environment.

A large number of studies have been carried out based on analysis of larval stomach contents, but there are large differences in methods used and hence there are a number of problems in interpreting and comparing these investigations (Heath and Lough 2007). In the studies parallel measurements of prey abundances in the environment are seldom carried out, and without such information it not possible to account for the specific feeding conditions or to estimate explicitly the preference for specific prey. Furthermore, the relative size difference between predator and prey is seldom recorded, even when this would provide the opportunity to compare organisms of different sizes. On the contrary the range between the smallest and the largest prey is often used to describe the preferred sizes of prey. Such measure provides very little information and is strongly dependent on sample size.

In my work, the analysis of larval feeding opportunities at sea is based on inspection of relative prey-size spectra. The work is stimulated by the hypothesis that this relative spectrum is constant throughout the growth of a larva (predator), an idea proposed as early as 1973 by E. Ursin (1973). The hypothesis has inspired much subsequent work, for example Pearre (1986) reviewed prey-size spectra and niche breadths of fish, showing a number of possible pitfalls when calculating and comparing these. He advocated for a use of the standard deviation of logarithmically transformed sizes of prey (the SLH-index) to express the width of the predator's prey size niche. Using this index he investigated a hypothesis suggesting constancy in the relative width of the prey size niche during predator growth. His findings supported such relationship, however the hypothesis is still much debated, and other studies describe systematic changes in the niche width during growth (Pepin et al. 1997). Pearre (1986) noted that the estimates of SLH might be biased if there were no consideration of environmental variation in prey sizes. However, both his own and a large number of other studies have solely used stomach contents to describe prey preferences, and what a predator eats and what it prefers are often confused in literature.

While my experimental work focused on behavioral aspects of the prey-size spectrum [6], the prey preference investigations involved larvae sampled in the field. Hence, here I considered "de facto" consumption in the natural environment. The goals were to examine larval abilities and preferences in a varied feeding environment using simple model considerations (Section 3.1 based on [10, 17]), estimate spatial variation in prey availability (Section 3.2 based on [6, 10, 11, 18]) and ascertain larval predation pressure on given prey organisms and the potential for larval density dependence (Section 3.3 based on [8, 11]).

3.1 Prey preference

A given preference for a specific prey organism denotes the extent to which this prey is preferred compared to other organisms. A quite long series of preference indices have been formulated, starting with Ivlev's index of electivity (Ivlev 1961). Most of the indices have subsequently shown to be of limited utility, but an index suggested by J. Chesson (1978) has found wide acceptance. It is simple, intuitively understandable and robust to the biases that many other indices suffer. It derives from a simple stochastic model of prey detection and prey catch following detection, and thereby links to the work on prey search described in section 2.1. It expresses for a given prey type (i) the ratio (α_i) between the amount (or relative amount) of prey in the diet (d_i) and in the environment (p_i), scaled such that $\sum\alpha_j$ for all prey types (j=1 to m) accumulates to 1:

$$\alpha_i = (d_i/p_i) / (\sum d_j/p_j) \quad (j=1\ldots m) \qquad \text{Eq. 5}$$

This index was used to describe the larval prey preferences in studies [10] and [17]. In [10] we sampled cod larvae of different sizes along with their potential prey in the northeastern North Sea. The gut contents of these larvae were examined in order to ascertain to what extent prey type and prey size influence the preference of larvae. In parallel, the material was used to investigate whether the relative prey size spectrum could be assumed constant during the larval life of cod.

Generally, copepods dominate in the diets of fish larvae (Last, 1980), and in the study copepods contributed more than 95% of items by number in the guts of investigated cod larvae. It should be noted however, exceptions are found when other plankton organisms appear to be of significant importance to given larval fish species (e.g. Sampey et al. 2007). The remains of the consumed copepods in the gut of the investigated larvae were mostly parts of their exoskeletons. Because of the process of digestion, much of the easily-digestible parts had dissolved, but the exoskeleton is much less digestible and remains in the gut longer. Most of the species characters of copepods are visible on their exoskeletons, and it is possible to identify the species (or genus) of prey even after an

extended period of digestion.

We were able to identify large fractions of the stomach/gut contents to six genera of copepods: *Calanus*, *Pseudocalanus*, *Paracalanus*, *Temora*, *Acartia* and *Oithona*. Preference indices for each of those genera were calculated and binned into 12 log-scale size classes using Eq. 5. The total number of classes was 72, and the calculations were carried out for five size groups of larvae. The resulting indices provided the possibility for a comparison of relative preferences in combinations of prey taxa, prey sizes and larval sizes (Fig. 7a). The combined analysis showed that both prey size, prey type and larval size had significant effects on prey consumption. At prey sizes above 800µm specific preferences for genera of copepods were evident. At these sizes the copepods have molted into late copepodite stages with large differences in post-molt behavior, and it is likely that differences in copepod escape behavior influenced calculated preferences of cod larvae. As was apparent in the experimental analysis [6] the effective clearance (consumption) of smaller prey is to a large extent determined by their visibil-

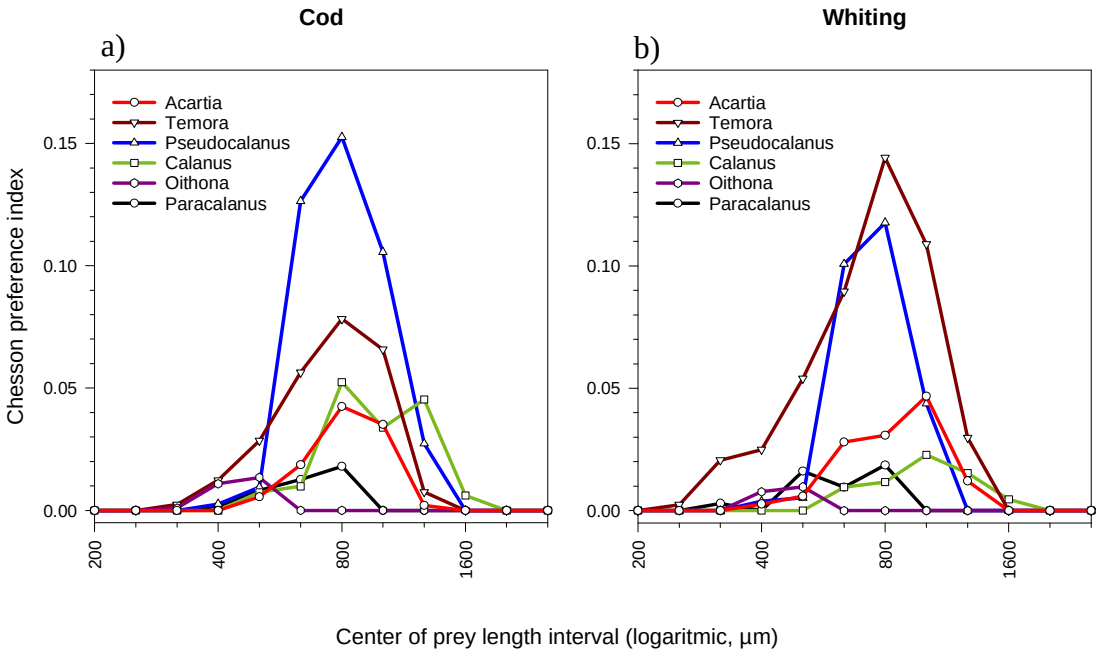


Figure 7. Prey preference spectra of cod and whiting larvae

Prey preferences of 15-25 mm cod (a) and whiting (b) determined from a combined analysis of prey size and prey taxa effect. All preference indices for each larval species accumulate to 1. For each prey species, larval size preference approximates a log-normal distribution. Larval preferences for prey species differed markedly even when prey were of the same size, and species preferences differed between cod and whiting. Results for cod [10], whiting (P.Munk unpubl. results).

ity, while for the relatively larger prey the clearance is mainly determined by escape responses.

The shapes of prey-size spectra were in good agreement with an assumed log-scaled size distribution (ref. Ursin 1973), and the widths and peaks of the distributions were calculated for a series of larval size groups. Their widths were described by an SLH index (ref. Pearre 1986) corrected for the composition of prey sizes in the Skagerrak. This analysis showed no relationships between the width of the relative prey size spectra and larval size, and so it supports the hypothesis that the relative spectrum remains constant during the larval life. The maximally preferred prey lengths, expressed in relative proportion to larval length, differed significantly among the investigated larval size groups, but it was on average 5% of larval length.

However, larval length is only an approximate descriptor of the capability for prey searching and consumption. Other morphological characteristics are important to larval feeding. The larval body shape is of importance for actual prey search, and mouth size puts an upper limit on the size of animal that can be consumed (Govoni et al. 1983, Sabates & Saiz 2000). Larval search and feeding capacities develop continuously during growth; mouth size increases and maneuvering skills improve. We expect larvae to become more effective predators through time, and based on such considerations it is commonly assumed, *a priori*, that relatively more food will become available during growth. It should be noted, however, that on the same relative scale the size and swimming ability of the potential prey also increase, and the improvement of larval prey search capability would often be counterbalanced by parallel development of the prey's escape ability. Concurrently, the "food value" of given small organisms declines as larvae increase in size. Even when those small organisms are an easy catch, excessive energy may be needed to catch each of them, and the larvae likely will come to prefer larger prey providing more nutrition from each successful catch.

The importance of morphological changes during development, and the morphological differences among larvae, were treated in a comparative study of four different tropical fish larvae from the Andaman Sea [17]. These larval species, identified to genera level: *Scorpaenoides* sp, *Carnagoides* sp., *Acanthocepola* sp and *Cynoglossus* sp. were obviously of very different morphology (Fig. 8), and even when they were collected within the restricted areas of the investigation, each species exhibited a wide size range. Therefore, the samples were well suited for study of differences in prey preference among morphologically different larvae.

The dominating prey items for all the tropical larvae were copepods (>98%), but there were huge differences in the taxonomic composition of the copepods eaten by each species of larvae (Fig. 8). Furthermore, the relative contributions of various prey taxa

changed during larval growth. Foer example, for all the species of larvae the relative amounts of Calanoida tended to increase at the expense of Harpacticoida as larvae increased in size. The changes, apparent from preference indices, were to some extent based on size differences between groups of copepods, although significant differences in taxonomic preferences were seen even within the same prey size interval. Prey

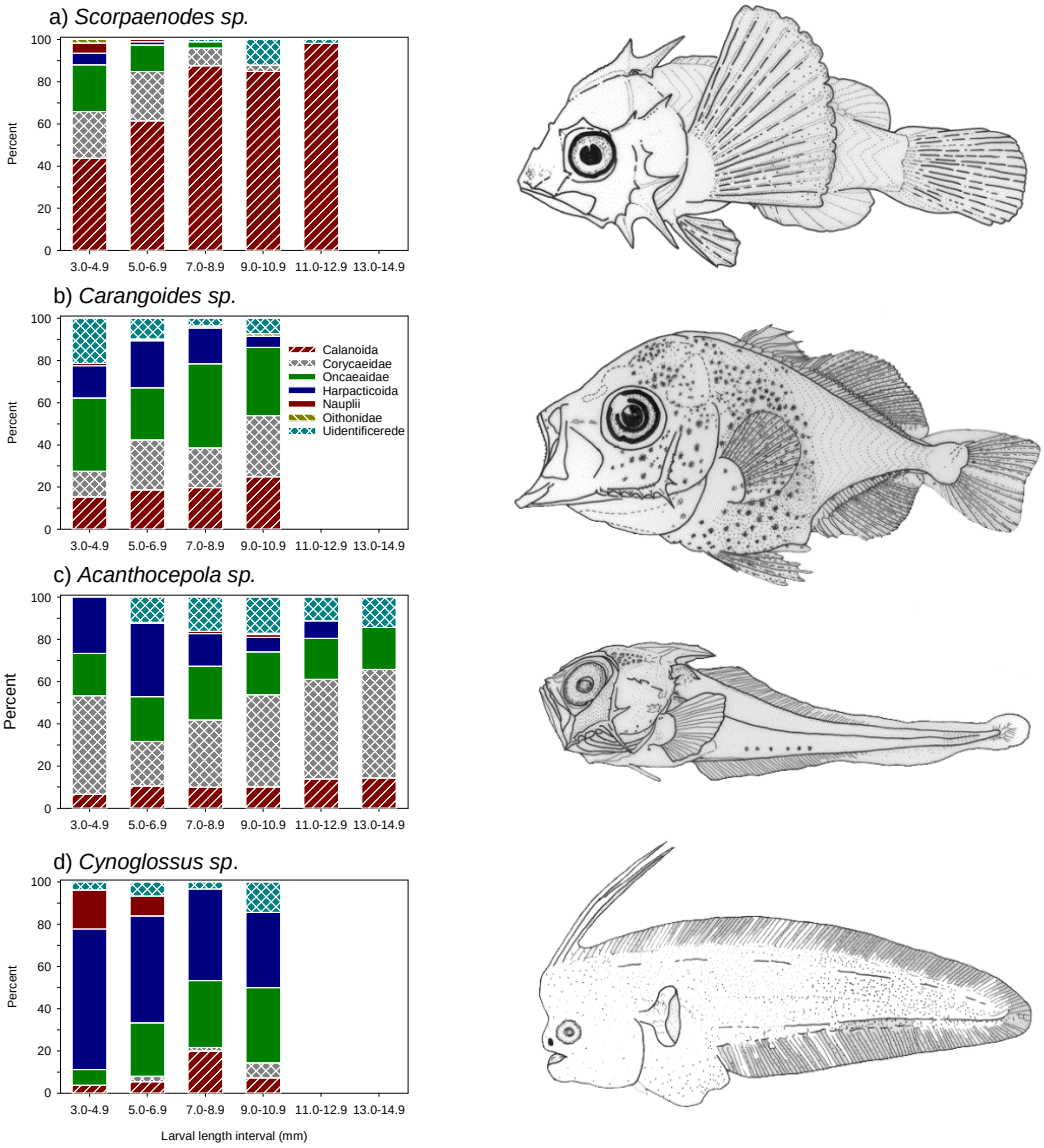


Figure 8. Taxonomic differences in prey consumption of larval fish species and sizes

Diet found from stomach content analysis of four tropical fish larval species. Prevalence of different copepod taxa are illustrated in a series of larval length intervals (mm). Proportion by number of prey items accumulates to 100% within larval length interval. Composition differed among size groups and larval species, and gradual changes in relative importance of prey during larval ontogeny are evident. From [17]

from the family Corcaeidae (*Corycaeus* sp. and *Copilia* sp.) were, for example, generally highly preferred, while Calanoida were only highly preferred by *Scorpaenoides* sp.

Hence, the preference spectrum of larvae from this study appeared as a combination of different taxonomic and size preferences, similar to the patterns seen for cod larvae as described above [10]. In addition, the study illustrated the huge differences among larval species in their taxonomic food preferences and there were, again, obvious changes in preferences during larval growth. Nevertheless, the prey preferences of fish larvae did show common patterns. When using the Andaman material to estimate the widths of the prey size spectra (SLH) as described above, we found that overall the SLH did not show significant increase or decline across the size ranges of these species. There were considerable variations in the estimated SLH's, but the averages calculated for the four species were of the same order (here 0.11 to 0.14 based on prey widths).

The four species of larvae showed different allometry. We measured jaw length and body height, both of which declined during larval growth relative to length in all species, but at different rates. Thus, we would not expect 'larval length' to be appropriate as a proxy for feeding capability during the entire larval stage of these fishes. We also observed that the relative size of preferred prey declined during growth of all species. When comparing the relative size of maximally preferred prey to larval mouth width, we only found a constant relationship across stages for one of the investigated species. Hence neither larval length nor mouth size appears to be a sufficient descriptor of prey preference due to allometric shifts in body proportions during growth.

In the investigation of prey preference of field-sampled herring in the North Sea [6] and Greenland halibut (*Reinhardtius hippoglossoides*) and sandeel (*Ammodytes* spp.) off West Greenland (Simonsen et al. 2006) we followed the same analytical approach as above. For those three species we found no change in the width of the relative prey size spectrum (SLH) during growth. The relative size of maximally preferred prey was constant for herring and sandeel but declined for halibut. Seen together this series of investigations ([6,10,17], Simonsen et al. 2006) in which the calculation of SLH was based on preference indices, provides good support for the *a priori* hypothesis that there is no increase in the (relative) feeding opportunities due to the ability to include larger prey during larval growth. Feeding opportunities depend to a large extent on the availability of particular prey sizes in the environment. Further, the results illustrate the applicability of the simple modelling considerations behind the relative prey size spectrum. Using that as a starting point, the different factors influencing larval feeding and preferences can be ascertained, and a modelled spectrum of a given combination of prey and predators can be used to predict feeding opportunities under given environmental conditions.

These relationships among preference spectra, prey availability and consumption are considered further in the following section.

3.2 Prey availability and consumption

The first theories about so-called biomass size spectra were published in the 1970s (Sheldon 1972, Kerr 1974, Sheldon et al. 1977). A biomass spectrum is described by the accumulated biomasses of organisms within log-scaled size intervals, and a fundamental assumption of this theory is that the biomass would be equal among intervals in stable ecosystems, while peaks or lows might appear because of an imbalance in either the production of some size category of organisms or in the predator-prey interactions (Cozar et al. 2008). This interpretation of the size composition of organisms in the environment is useful for the analysis of a predator's prey size spectrum mentioned above. Both the environmental and prey size preference spectra use log-scaled sizes, and we can estimate the relative amount of biomass available to a predator by comparing its preference spectrum to the available biomass spectrum (Fig. 9).

During the investigations of larval fish diet preferences [6, 10] and the prey potentially available to them [11, 18] we calculated the biomass spectra for the immediate environment. These deviated substantially from an "ideal" flat spectrum (ref. Sheldon 1972). Both peaks and lows were seen across the size intervals of larval preferences, and specific sizes of prey could be very poorly represented at some stations. Note, though, that these biomass spectra were based solely on copepods which dominated the size fraction from 0.2 to 2 mm. The abundances of other taxonomic groups smaller than 0.2 mm were greater than appeared from samples, and biomasses in that range were hence underestimated.

An investigation of growth variation of cod larvae illustrates the extent to which the spatial variation in the species and size composition of potential prey influences the amount of food available [18]. In this study the influences of size- and species-preference were combined in prey availability calculations, and those illustrated the much greater importance of *Pseudocalanus* spp. as prey for 15 mm cod larvae than was evident from their immediate abundance. The relative importance of *Calanus* spp. declined when interpreted as prey available to the 15 mm larvae, however due to their high biomass they were still a significant part of larval diet. More general tendencies in the occurrence of the copepods were also reflected in the estimates of prey biomass available to larvae, particularly in areas at the periphery of the frontal zone with low abundances of larvae. Prey availability in those distant areas was less than 10% of what was estimated for the central areas.

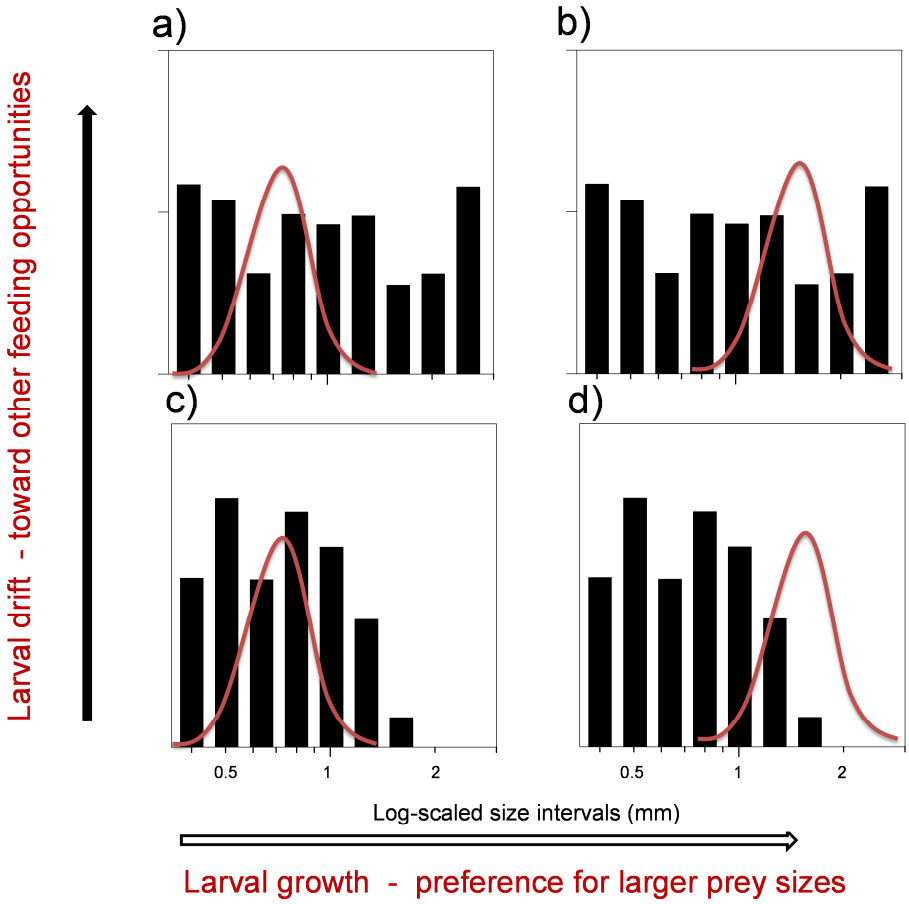


Figure 9. Schematic illustration of potential changes in prey availability to larvae

Biomass spectra illustrated by bars and preference spectra of larvae by red curves. Two different sites, upper panels a)-b) and lower panels c)-d) are shown. Two potential changes in prey availability are considered. One is caused by *larval growth* at the same site, which will move the prey preference spectrum to other parts of the biomass spectrum of potential prey. This would have less effect at the a)-b) site than the c)-d). The other is caused by *larval drift* into other areas where the biomass spectrum differs. This with be of less effect for the a)-c) larva than for the larger b)-d) larva. Based on [10].

A change in available biomass due to changing species- and size-composition of copepods is reflected in the actual amount of biomass consumed by larvae. Assuming that the quantities of exoskeletons in the guts reflect the amounts of copepod biomass consumed during a given feeding period, we can compare them to biomasses available in the prey field. Such a comparison was carried out for cod larvae during two years of investigation, 1994 and 2001, years when biomass of larger prey organisms differed substantially in the same sampling area (Fig. 10). The calculated biomasses in this comparison illustrate that absence of larger copepods (as in 2001) leads to a decline in

possible consumption for the larger larvae. While larvae shorter than approximately 20 mm had almost the same average stomach content of about 2% of their own weight in both years, the average content rose to around 4% for the larger larvae that were distributed where large copepods were available in 1994. In 2001 gut contents stayed at about 2% for all sizes (P. Munk unpubl. results). Hence, for cod in the investigated area low availability of big copepods may have severe consequences for a given year class of larvae, due to suboptimal feeding opportunities when larvae reach lengths greater than approx. 20 mm.

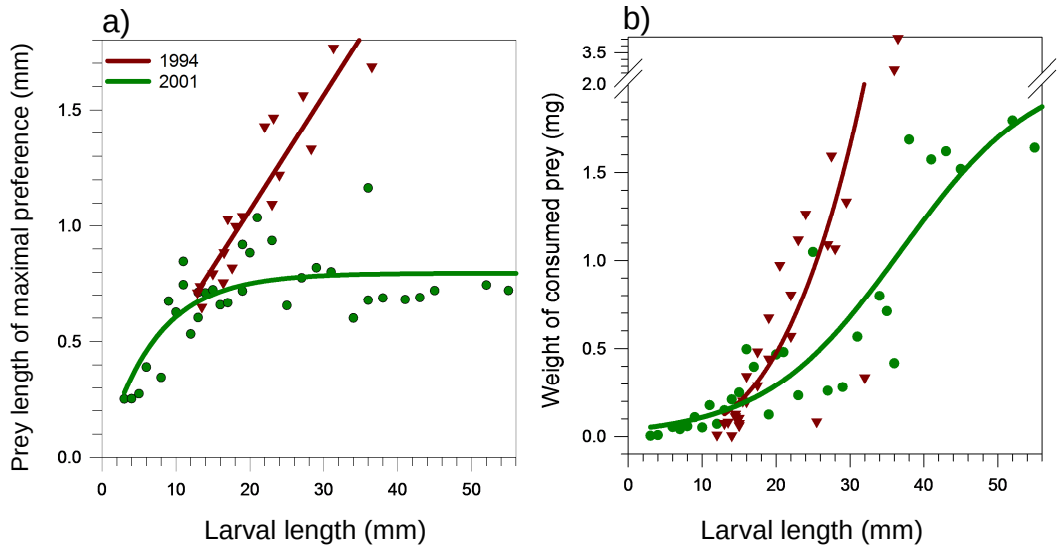


Figure 10 Differences in feeding opportunities of cod larvae between two years.

Comparison of preference and consumption estimates for cod larvae distributed in the same area of Skagerrak in 1994 and 2001. a) Larvae sampled in 1994 had a wide range of prey sizes available, and their calculated preference maxima increased with larval length. In 2001 there was not sufficient large prey in the surroundings to describe the size preference of the larger larvae, seen as a constant level of "maximal preference" at larval lengths above 20 mm. b) This failure of fulfilling larval preference spectra is reflected in the amount of biomass consumed, in 2001 the biomass in stomachs of larvae above 20 mm was much less than seen for larvae in1994. Results from 1994, [10], and from 2001, (P. Munk unpubl.).

3.3 Prey production and density dependence

When assessing the available biomass, as reported above, this is interpreted as a quantity available for an individual larva at the time of sampling. Over time, production of new prey is essential in order to sustain the prey density and thus the consumption

rates of the larvae. While the larvae from a given year-class grow as a cohort of predators of approximately the same size and needs, they can exert great predation pressure on preferred groups of prey, potentially influencing their own food resource. This would result in density dependence, because an increased density of larvae results in less prey available for each larva. Added to that, a number of larval species might share the same areas and if their prey preferences and spatial distributions directly overlap, they might compete for food.

These questions about potential density dependence as a consequence of prey competition have implications for the understanding of opportunities in the larval life of fish and for understanding variable recruitment to the stocks. Thus these issues have been much discussed (e.g. Fortier & Harris 1989, Cowan et al. 2000). In freshwater and estuarine ecosystems, both fish larvae and planktivorous fish have been shown to impact the biomass and species/size composition of the plankton community (Brooks & Dodson 1965), while there is less evidence for similar top-down effects in the open sea where ecosystems can be more complex. In the sea there is large biodiversity, and there are significant spatial and seasonal variations in the composition of the plankton community. Some predatory and prey species prevail in the spring, others in the autumn, while yet others are of more or less constant abundance through the seasons.

As illustrated above, the variation in sizes and species in the plankton influences their availability to fish larvae as prey, and in turn influences the predation pressure from larvae on preferred fractions of the plankton. In two studies of the plankton community in the central North Sea, one in early summer and one in autumn, we investigated the community of copepods and fish larvae, focusing on the predation pressure exerted by larvae, and the possibilities of larval feeding being influenced by their own density [8, 11]. Emphasis was put on abundant, potential predator and prey organisms and on the spatial and seasonal variation in respective abundances. The significance of spatial variation was considered by including the large variability in plankton communities across a hydrographic front in the area of Dogger Bank, and we inspected the “seasonality” in conditions by comparing the summer and autumn investigations. Predation pressure from each of the common fish larval species was evaluated based on comparisons between larval preference spectra and the biomass spectrum of copepods and cladocerans that included both taxonomic and size effects. Based on estimated consumption rates we calculated the proportion of the available plankton biomass the larval fish community would consume per day. In a stable situation the consumed biomass should be replenished by the egg production of the copepods, eggs that subsequently hatch and grow to the relevant naupliar and copepodite sizes in the available food spectrum. Because there is a fairly strong relationship between the egg production rates and copepod growth rates during later stages (Kiørboe & Johansen 1986, Berggreen et

al. 1988), we used egg production as a measure of the replenishment of prey within relevant prey size intervals. The predation pressure on a given fraction of potential prey was then expressed as the fraction of the production that was consumed.

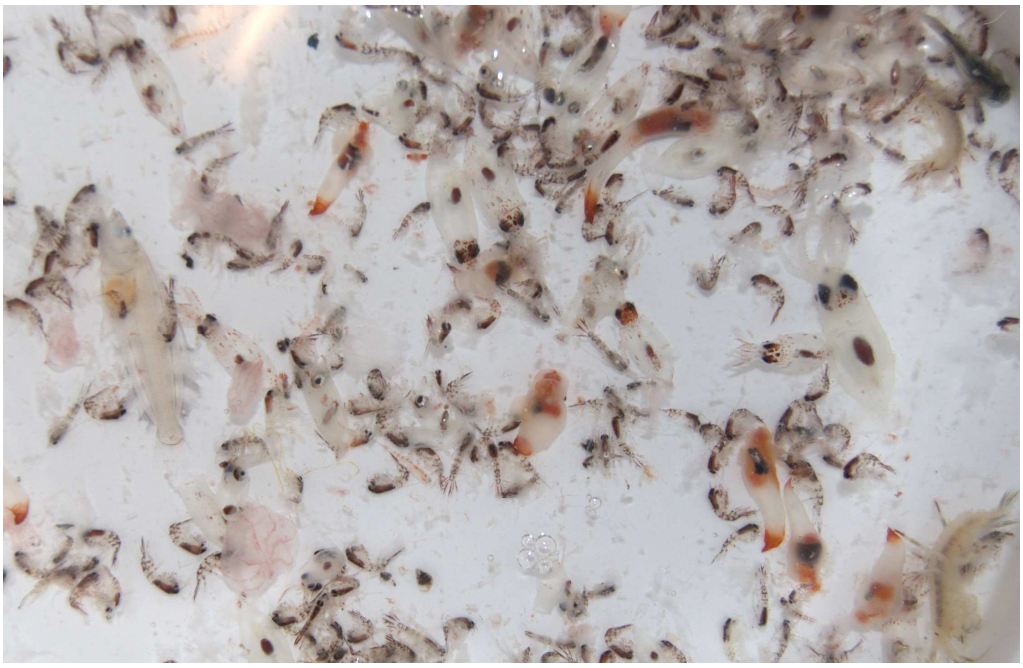
Both investigations covered a tidal front at Dogger Bank where the plankton community composition changed across the front. In the early summer the shallow side of the front was dominated by neritic copepods such as *Acartia* spp. and cladocerans like *Evadne* spp., while whiting dominated among fish larvae [8]. The configuration changed across the front and at greater water depths, copepods including *Pseudocalanus* spp. and *Calanus* sp. were abundant, while cod became the most abundant fish larvae. Estimates of the relative prey consumption by larvae followed this change in plankton composition, in the shallow area whiting were responsible for 73% of the consumption, while in the front cod larvae accounted for 40% of total consumption. When comparing the estima-ted total consumption and the measured production in the respective sub-areas, we found quite low predation pressure on the relevant size intervals of prey: 1-7 % of the daily production in the shallow area and 3-11% in central areas of the front. Thus, this investigation indicates that in the early summer, when primary and secondary productions are generally high, the predation by fish larvae has marginal influence on the abundance of their food resource.

The investigation carried out in September indicates that the conditions may change across seasons [11]. Algal abundance was less than observed during the early summer, and egg production had declined. Moreover the plankton community had changed. Abundance of *Acartia* spp. had declined on the shallow side of the tidal front, and all areas investigated were dominated by *Pseudocalanus* spp, *Paracalanus* spp and *Calanus* sp. There were still some whiting larvae present, but other larval species had replaced most of the species observed during the earlier period. The now predominant larvae were sprat and lemon sole (*Microstomus kitt*). Total predation pressure reached 3-4% d^{-1} of the biomass of potential prey in preferred sizes, while the copepod production was estimated to be 3-7 % d^{-1} of the biomass. So, this study suggests that under certain circumstances, the food resource of fish larvae cannot be replenished at rates as great as their consumption. The relatively high predation pressure was due to extraordinarily high abundances of sprat larvae, and hence the investigation points to the possible consequences of situations when abundant cohorts of relatively identical larvae all feed on a restricted fraction of the plankton organisms in their environment. In such cases density dependence is possible.

The possibility that fish larvae influence their food resource when they are in exceptionally large abundances shortly after hatching is supported by calculations made for the herring-spawning grounds [3]. Here the predation pressure was calculated from esti-

mates of clearance rates in the laboratory studies on herring larval prey search [1] and estimates of consumption were compared to estimates of copepod production. While the two estimates show wide variation, they were of the same general magnitude and thus indicate that density dependence can occur for these patches of herring larvae, especially in their centers.

In respect to density dependence effects *among* species, these will only occur when there is significant overlap in species' prey preference spectra. There is often a distinct spatial separation between species of larvae, as observed both from depth-integrated sampling across frontal zones and from vertically stratified sampling in the water column [8, 12, 21]. Significant separation between species is also suggested by the marked differences in species composition of consumed prey [11, 17], differences that could stem from differences in prey distributions, morphologies and behaviors. Hence, from the generally low predation pressure estimated for larval groups, and from indications of high degrees of niche separation among species of fish larvae, competition for food does not appear to be an important factor in the lives of fish larvae.



Mixed catch from a 2-meter ring net launched in Godthåbsfjorden Greenland

The plankton is generally of larger size in the Arctic. And because of the low temperature of water, the degradation of organisms is relatively slow. Here a large larvae of Greenland halibut (Reinhardtius hippoglossoides) (flatfish central, left) is found together with nudibranchs (orange), amphipods (black), cephalopods (two large eyes) and copepods (small, transparent). Own photo.

4 GROWTH AND MORTALITY

Fish larvae are particularly effective at converting consumed food to somatic growth. Investigations we carried out using small herring larvae (Kiørboe et al.1987) showed a linear relation between consumption and growth at low rates of consumption. This relation levels off at higher values, probably because of declining assimilation efficiency, but the initial linear part of the relationship suggests growth efficiency close to that theoretically possible. Other studies of small juvenile fish show a somewhat lower efficiency, and there seems to be an inverse relation between the efficiency and the size of the fish; not because of size in itself but due to a declining specific growth rate with increasing size (Kiørboe et al. 1987). The mortality rate in the early larval stages is considerably larger than seen for juvenile fish (McGurk 1986), thus prioritization of a high initial growth rate is reasonable in an ecological and evolutionary context.

Even small differences in growth rates may lead to great variations in the amount of surviving larvae (Houde 1989). Further, models of larval growth and survival illustrate not only that the average growth of a cohort of larvae is of significance for the final survival to recruitment, but also the variation among growth of individuals in the cohort is of importance to the overall survival (Cowan et al. 1996, Pitchford et al. 2005). The variability is introduced by the variable environment, and the studies indicate that the greater variability the higher the survival probability.

Thus, studies of larval growth performance provide essential information for our understanding of larval fish ecology. The studies were greatly advanced in the 1970's by the appearance of a new technique providing unique information about larval age and day-to-day growth trajectories. The method is based on analysis of fish larval otoliths, three pairs of calcium and protein containing stones that are a part of the auditory labyrinth system (Fig. 11). Two of the otoliths, astericus and lapillus, are relatively small, while the sagitta is bigger throughout the fish's life. For more than a hundred years only the seasonal variation in material deposition in otoliths was acknowledged and used for ageing of fish on a scale of years. In 1971 it was discovered that deposition takes place in a daily rhythm that can be ascertained in fish below three years of age (Panella, 1971). Depositions on the otolith depend on the metabolic rate of the fish, and processes are interpreted as daily metabolic changes leading to more or less deposition of aragonite (a calcium mineral) in the protein matrix of the otolith. However the metabolic rate can be changed by factors other than the daily cycle, and the degree of coupling between otolith and somatic growth is much debated (e.g. Campana 1990, Barber and Jenkins 2001). Further, it has been strongly debated whether deposits during

very low somatic growth could be negligible and difficult to see by ordinary microscopic examination, leading to severe underestimation of age and thus overestimation of growth rate.

In my investigations of linkages between environmental factors and growth of fish larvae, emphasis was put on covering a wide range of spatial scales across which the variation in conditions could be expected to influence larval growth. As emphasized later, areas of larval distribution coincide with frontal zones that, by their very nature, encompass huge variation in physics and chemistry. By covering this variation in cross-front investigations, I examined variation in growth across hydrographic features for larvae of sprat (*Sprattus sprattus*) and cod (Section 4.1 based on [7, 18]). Other investigations focused on larger scale differences between cohorts of herring larvae dispersing and drifting from spawning grounds off Scotland and into central areas of the North Sea (Section 4.2 based on [3, 5]). Fundamental assumptions in the interpretation of larval growth rate and the later recruitment have been that growth and survival are linked and that growth variation will be reflected in the mortality rate.

Specific mortality rates and the relation between growth and mortality were examined during investigations on larval cohorts of herring and cod in the North Sea and sandeel (*Ammodytes spp.*) at West Greenland (Section 4.3 based on [3, 13, 15]).

4.1 Variation in growth rate across hydrographic features

Many larval nursery areas coincide with fronts or comparable oceanographic discontinuities. Steep changes in physical and chemical conditions over short distances are observed in such areas, so in order to examine growth variability within the nursery area, it is necessary to resolve it at the scale of the frontal structures. Growth rate estimation based on otolith examination provides such an opportunity. There are some preconditions for the use of the method, of which the most important are that number of rings and age in days correspond, and correspondence in growth trajectories among fish larvae sampled at a given station. The length increase during the larval stage often follows a curvilinear path described well by the Laird-Gompertz curve (Laird, 1969). This expresses exponential growth in size, but with the growth exponent declining with age. This curve is founded on basic growth considerations (Savageau, 1979).

Thus, for samples of larvae for which we had length and age information, we carried out a non-linear fit of the Laird-Gompertz formula expressed as:

$L_t = L_0 \exp(\beta(1-\exp(-\alpha t)))$ Eq. 6

Where L_t is the length (mm) at age t (days); L_0 is the initial length, α is the instantaneous growth and β is a dimensionless parameter.

Growth rate at a given time is found from differentiation of Eq. 6:

$dL/dt = L_0 \beta\alpha \exp(\beta(1-\exp(-\alpha t))-\alpha t)$ Eq. 7

The growth rate at a given length (L_m) can be estimated by first assessing the age, t, when larvae were at length L_m from Eq.6 , and then inserting this age in Eq. 7.

When comparing growth rates, it is appropriate to look at specific rates of growth and express this by weight, and the weight specific rate of growth (SGRW) may be found from the length specific growth rate (SGRL) as:

SGRW= b SGRL Eq. 8

where b is the exponent of the species length-weight relation.

This method of estimation was used in the investigation of growth variation in the distributional areas for sprat and cod in the North Sea [7, 18].

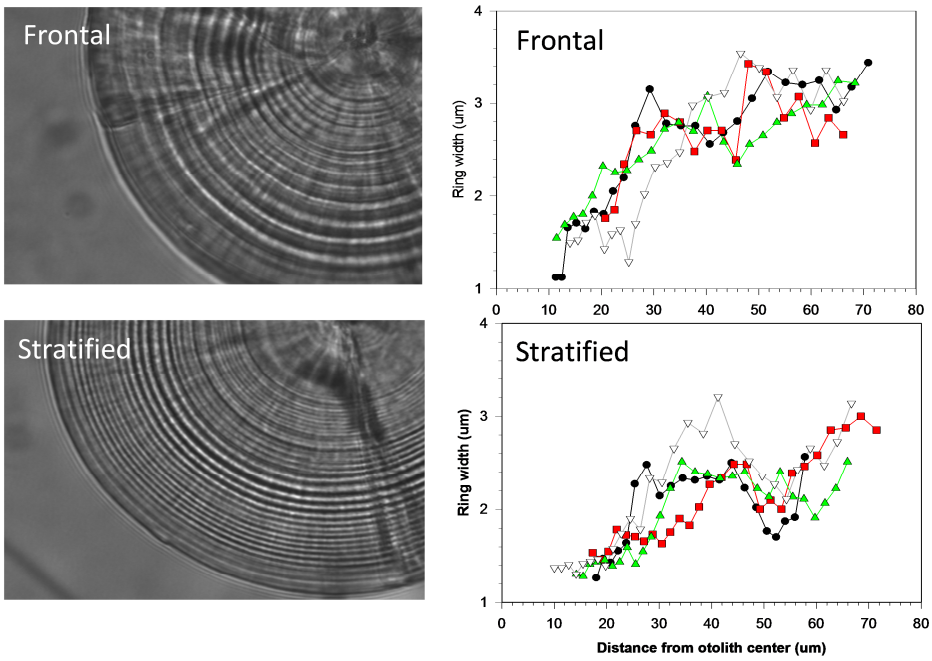


Figure 11. Different growth patterns in otoliths of sprat larvae.

Marked differences in ring structure were apparent in sprat otoliths from different areas in the eastern North Sea. In the area of the hydrographic front, the rings were of steadily increasing width, while in the more offshore stratified regions the ring widths were generally narrower and showed a characteristic decline between ring 40 and 55. Such ring width measures illustrate that not only integrated growth might differ between areas, but also the daily growth trajectories could show systematic patterns and differences (P. Munk unpubl.).

Growth of sprat larvae in the German Bight of the North Sea [7]

An important nursery area for sprat is found in the German Bight of the North Sea, and an analysis of growth variation in larval sprat was part of a larger field investigation of conditions for fish larvae in the eastern part of the North Sea [7]. Sampling was carried out in August 1989 along a number of east-west transects primarily running from shallow areas to deeper and crossing the estuarine front between central North Sea water and the freshwater-influenced coastal zone (the Jutland Current). Sprat larvae have a very distinct ring structure in their sagittal otolith (Fig. 11), and otoliths of sampled larvae were dissected, mounted in resin on slides, and the otolith rings were counted under a microscope. Due to poorly measureable length of larvae I wanted to convert otolith size to larval size. Such conversion might, however be biased by differences in growth rates and/or temperature conditions (Barber & Jenkins 2001). I therefore tested whether the fast growing larvae (described by age-length relations) had relatively smaller otoliths than slowly growing larvae. This was not the case, and neither did temperature influence the relationship between somatic and otolith size. Thus, in the study I used otolith size as proxy for larval size.

The estimates of growth rates of sprat larvae differed among stations, even between neighboring stations only 16 km apart. A significant change was seen when crossing the frontal zone; growth rates declined from coastal stations toward deeper, stratified water (Fig. 12a). Further, there was a tendency to generally higher growth in the northern part of the investigation area, along the frontal zone. The decline in growth rate across the front was stronger for the larger larvae. For instance, the specific growth rate (SGRW) for 12 mm larvae declined from approx. 0.16 to 0.12 d^{-1} along the transects, whereas the decline was from 0.11 to 0.03 d^{-1} for 16 mm larvae.

The investigation linked growth rate estimates directly to the observed hydrography. Even though the highest growth rates were found in areas with weak stratification of the water column (i.e. at low values of calculated stability parameter for the water column), we could not prove an unambiguous connection between water column characteristics and attainable growth rates. The central front zone, the section where the horizontal changes in hydrographic measures were greatest, did not show a discernible peak in the estimated larval growth rates. Some of the highest values were found at stations very close to the coast. However, a linkage was indicated between attainable growth rates and primary productivity at sampling stations. Growth rate estimates increased along with rising algal concentration, measured by the amount of chlorophyll *a* in the water, up to a chlorophyll level of 120 mg m^{-2}, at which additional concentration had a negative influence on growth rates.

The relationship between growth rate and potential prey was also examined. Copepod abundance estimates were available at eight stations of the stations, and food availability calculated for a 12 mm sprat larva showed positive correlation to the respective estimates of larval growth rate.

Growth of cod larvae in the northeastern North Sea [18]

Later investigations in the areas of cod larvae distribution in the northeastern North Sea (just north of the sprat nursery area) during the month of May 1992-1994 provided an additional possibility to examine mesoscale variation in attainable growth rates of fish larvae [18]. The sampling during the field surveys covered the full breadth of the frontal zone and of the cod larvae distributions, and part of the sampling was used for estimation of prey preferences of cod larvae [10]. The feeding opportunities were at their highest in central parts of the frontal zone, and the major goal of the study was to examine whether there was a simple, direct connection between estimated prey availability and estimated growth rates of cod larvae.

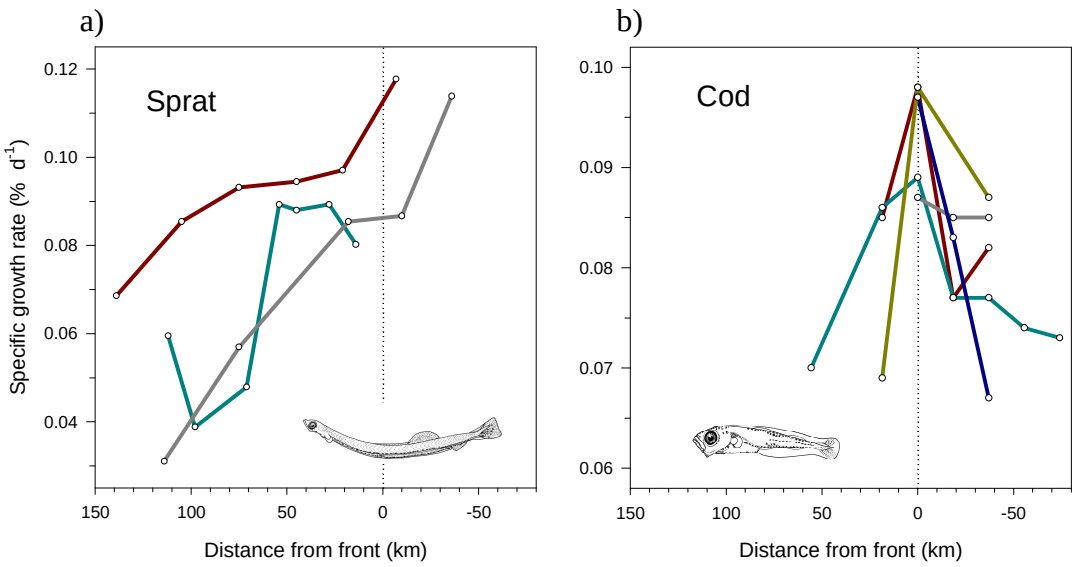


Figure 12. Growth rate variability of fish larvae across hydrographic front zones

Estimates of specific growth rate in weight (SGRW) are shown for sprat and cod larvae in the German Bight (1989) and the Skagerrak (1992), respectively. For both species the curves illustrate estimates along different cross-frontal transects (distance zero at central position of frontal zone, negative inshore and positive offshore). a) For a 16 mm sprat larvae growth rate declined dramatically from the central part of the frontal zone and away from the front in the offshore direction. b) For a 15 mm cod larvae the growth rate estimates peaked in the identified central area of the frontal zone on all transects. The results for sprat are from [7], for cod from [18].

Cod larvae from a number of selected sampling transects were dissected, and their otoliths were analyzed. The daily periodicity of ring formation has been verified in cod larvae (Geffen 1995), and age in days was estimated from the ring counts. For each station, a non-linear fit to the age-length information was carried out using Eq. 6, and growth rates were estimated for size groups of larvae using Eq. 7 and 8.

In earlier analyses of the hydrography in the area [12], we defined central areas of the front based on the vertical stratification Growth rate estimates for various sizes of cod larvae were then correlated to their respective positions in the frontal zone (Fig. 12b). Generally, we found a declining growth rate with size of larva, but at all sizes the growth rate peaked at the station defined as "central" in the frontal zone. The decline in growth rate away from the front, in both the offshore and the inshore directions, were significant and the growth rates differed significantly among the years of investigation (1992-94) and between transects. The estimates of growth (specific in weight, SGRW) were between 0.07 and 0.11 d^{-1} for 15 mm cod larvae. Obtainable growth rates depend on temperature, and in other areas with generally colder temperatures the SGRW's are generally lower, approximately 0.08 d^{-1} at Georges Bank (Bolz & Lough 1988) and 0.04 to 0.085 d^{-1} at Browns Bank (Campana & Hurley 1989). However, in the present field study we did not find that the variability among growth rate estimates had any significant relationship to temperature, not in either the spatial or the annual variations.

In this study there was no significant correlation between the estimated growth rates and the estimated availability of prey. Even when we found a correlation between both these estimates and frontal characteristics, we could not demonstrate a direct correlation between prey availability and obtained growth. This may be due to limitations of methods; our estimates of prey availability were made at the time of sampling, while the method for calculation of growth rate was based on a whole-life record of obtained growth rates. In addition factors such as water density and turbulence might interfere. These are both related to frontal processes, and experiments have shown that they influence larval feeding and growth (Section 2.4).

4.2 Variation in growth rate among cohorts and regions

Growth estimation of herring larvae based on cohort tracking [3, 5].

The studies on nursery areas of herring larvae have provided the possibility to inspect growth rate variation from the mesoscale (10s of km) to macroscales (100-1000 km). During September-October 1985, we followed cohorts of herring larvae hatched over

several banks off Scotland [3]. By surveying their distribution patterns early after hatching, we could delimit specific cohorts that we followed during later surveys. During the period of investigation the spatial overlap between cohorts became more and more obvious, but by examining larval length distributions, we could separate the cohorts from survey to survey. Because of the displacements among the size distributions of cohorts, the mix of larvae from overlapping cohorts was discernable as peaks in the overall size distribution, and cohorts could be separated. The average growth rate of each cohort was then calculated from the temporal changes in its average length at central stations of the distribution. This method has some uncertainty, being dependent on how precisely the cohort center was identified, but there was good consistency in the length estimates, as they all showed a linear rise over time.

The linear growth rate estimates were between 0.13 and 0.24 mm d^{-1}, corresponding to a SGRW between 0.045 and 0.075 d^{-1} for a 12 mm herring larva. These estimates are significantly lower than the SGRW estimated for a 12 mm sprat larva (0.12-0.16 d^{-1}), but are similar to estimates from a number of other studies on herring larvae (in Kiørboe and Munk, 1986). Differences between cohort estimates indicate differences among environmental conditions for the larvae on the specific banks, even though all the banks are in hydrographic frontal zones. We estimated prey availability along two transects based on an occurrence of copepods in two size intervals, but those estimates did not show a relatively larger feeding opportunity in the area inhabited by the fastest growing cohort.

During the period of investigation in 1985 [3], we found the cohorts of herring larvae from the separate spawning sites became more and more mixed, to the extent that the original cohorts were difficult to separate. However, the various spawning sites for the whole (meta) population of the autumn-spawning North Sea herring are assembled in regional spawning areas. These areas are sufficiently geographically separated to make it possible to follow sub-populations of herring during the following winter months. Hence the tracing of herring groups could be continued to ascertain growth differences among those spawning areas – in this case on a macroscale (regional) level. We carried out such an investigation on the yearclass of herring larvae spawned in 1987, which we followed from September 1987 to February 1988 [5]. International cooperation using several research vessels made it possible to cover most of the distribution of herring larvae in the North Sea. Larvae from specific regions could be identified from patterns in length distributions and abundance, and the interpretation was supported by a modelling exercise that ascertained the drift from the spawning areas to nursery areas (Bartsch et al. 1989). Analyses of growth rates obtained for larvae from sub-populations were based on the delimitation of distributions within a southern, a central and a

northern region with a further separation of the northern region into an eastern and western part.

Growth rate estimations based on size changes in delimited groups of larvae over time and estimations based on otolith analysis of members of groups both depend on a range of assumptions, and both have some inaccuracy. This investigation of regional variation in growth rates [5] focused on otolith examination for the analysis of growth; however, the large number of surveys provided an additional opportunity to investigate growth by changes in length for separate groups of larvae and to compare results from the two methods. For the analysis growth from size distributions, we assumed that the length distribution of all larvae within a regional area represented its sub-population and calculated the growth rate from the change in modal length during the investigation period. Average growth rates for specific sub-populations over the October-February period ranged from 0.11 to 0.16 mm d^{-1} (~ SGRW of 0.02- 0.05 % d^{-1}), with a significant difference between a relatively slowly growing northern sub-population and a relatively fast growing southern sub-population.

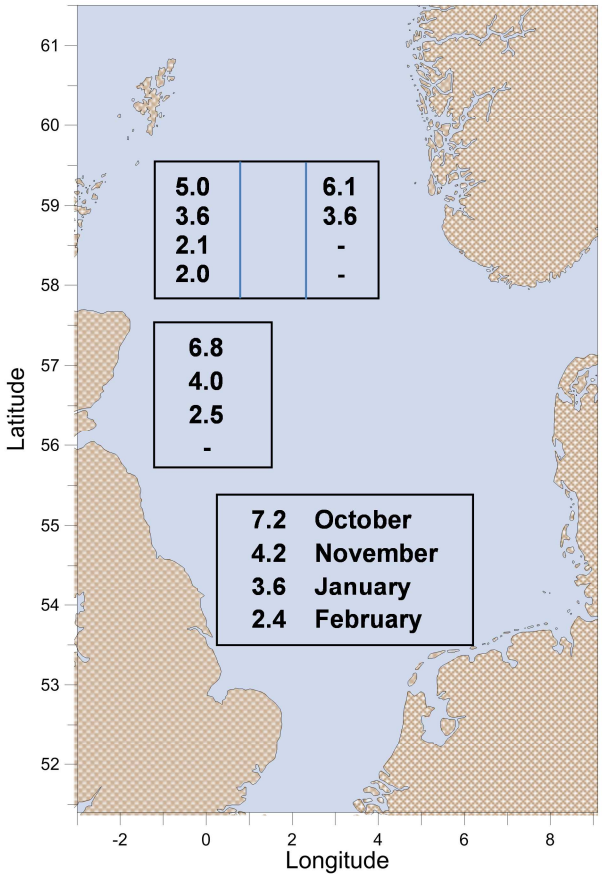


Figure 13 Regional differences in growth rate of herring larvae.

Larval specific growth rate in weight was estimated by otolith analyses of larvae sampled in different regions and different months of the year. Estimates for four months are listed in rectangles which encompass approximate area of sampling. There was a significant trend of declining growth rate during the fall/winter season, and within each month estimated growth rate declined from southern to northern regions. From [5].

Growth estimation of herring larvae based on otolith analyses [5].

The alternative method based on analyzing otolith ring structures does not depend on appropriate delimitation of the entire distribution and/or its center; the main assumption is that larvae had (approximately) the same growth trajectory. We used larvae from high density areas in each region and subsequently related the estimated growth rate to region and season. This method produced somewhat higher specific growth estimates (~ SGRW of 0.02 -0.07 d^{-1}) than the analyses of changes in average sizes, which could indicate some bias in the method due to underestimation of ring numbers (age at length). However, there was a good correspondence between a length increase from September to February modelled on basis of the monthly growth rate estimates in regions, and the obtained lengths observed in February, those ranging from 29-36 mm [5]. Overall, the growth rate estimates differed both among regions and between seasons (Fig. 13), and both the decline in SGRW during the entire period and regional differences in November were statistically significant. Furthermore, significant differences among regions in ring-widths, which also express growth rates, were found for the months of October, November and January.

These investigations illustrate the prominent growth rate variability in fish larvae, apparent across a range of scales. The differences determined at the regional scale indicate that attained growth might, nevertheless, be an ambiguous measure of "life quality". Despite the lower growth rates in the northern regions, those spawning areas contributed significantly to the entire North Sea herring population (Payne 2010). Other factors exerting influence at the population level need to be considered; the overall predation pressure might be lower in the north, or a lower growth rate (and survival) in the early stages might be compensated by enhanced conditions later. However, within a given population the growth of an individual would indicate its chance of survival. This will be considered next.

4.3 Mortality rates and the relation between growth and mortality

Larval survival to recruitment is the key information needed when assessing fish stock maintenance and management. However, measuring survival is a difficult task. We need to keep track of the number of individuals in delimited groups during extended periods of time, which is difficult in the open sea where distributional patterns continuously change due to larval vertical migrations, dispersion and drift.

Assessing mortality rates from patch studies – herring in the North Sea [3].

In the 1985 patch studies on herring larvae off Scotland our coverage of the distributions, often with very low abundance estimates at the periphery of the sampling, made it likely that we had covered significant parts of given cohorts of larvae [3]. Thereby we would be able to estimate the overall abundances and by comparing estimates from consecutive surveys ascertain larval mortality rates. In earlier studies in the same area [2], we had used 3D Gaussian distributions to estimate overall abundances, but the distributions of the 1985 cohorts could not be appropriately fitted by this theoretical distribution. As a simpler alternative we accumulated cohort abundances from each subarea of the 10x10 nautical mile sampling grid. In some cases it was evident that abundances also could not be estimated in this way, either because of poor coverage or of supplementation by newly hatched larvae. Those estimates were not used in the final comparison. In all, 15 estimates of abundance over time were made available for the estimation of mortality rates. We assumed an exponentially declining number of larvae and the same mortality rate for all larvae in the cohort. For one of the cohorts, the estimate was unrealistically low, but the other estimates were in a reasonable range from 0.03 to 0.05 d^{-1}. Regressions were consistent; however, the separation of cohorts might not have been accurate, and the estimates should be taken with caution. While this type of study provides valuable information about the level of larval fish mortality, it does not have the accuracy necessary for an analysis of mortality differences and the circumstances generating the mortality. An alternative method of ascertaining mortality differences would be to investigate the "characteristics of the survivors", to follow changes in certain characteristics of larvae in a cohort from one coverage to the next.

Assessing differential mortality from otolith characteristics – cod in the North Sea [15].

A characteristic, which we expect to be of great importance to larval survival, is the ability to maintain a high growth rate. A relatively high rate indicates a good and well satiated condition of the larvae, and moreover, the growth rate determines the duration of the larval stage and when larvae will reach stages of relatively lower mortality risk. (Anderson 1988, Houde 1997). The growth history of the larvae is recorded in the microstructure of their otoliths, and by representative sampling of larvae from the same population across its development, we may be able to evaluate whether the composition of larval growth histories has changed. The working hypothesis in such an analysis is that mortality of larvae with relatively slower growth up to the first sampling would be relatively greater than that of larvae with better growth rates. In that case slow starters would be under-represented at a second sampling compared to the first sampling.

This potential relationship was investigated during a study of cod larvae in the north-eastern North Sea in 2001 [15]. The study was part of a larger research program during which a series of sampling transects across a larger areas covered the plankton distributions from March to June. In the April and May surveys, it was apparent that we had achieved good coverage of a selected cohort of cod larvae, and we then examined

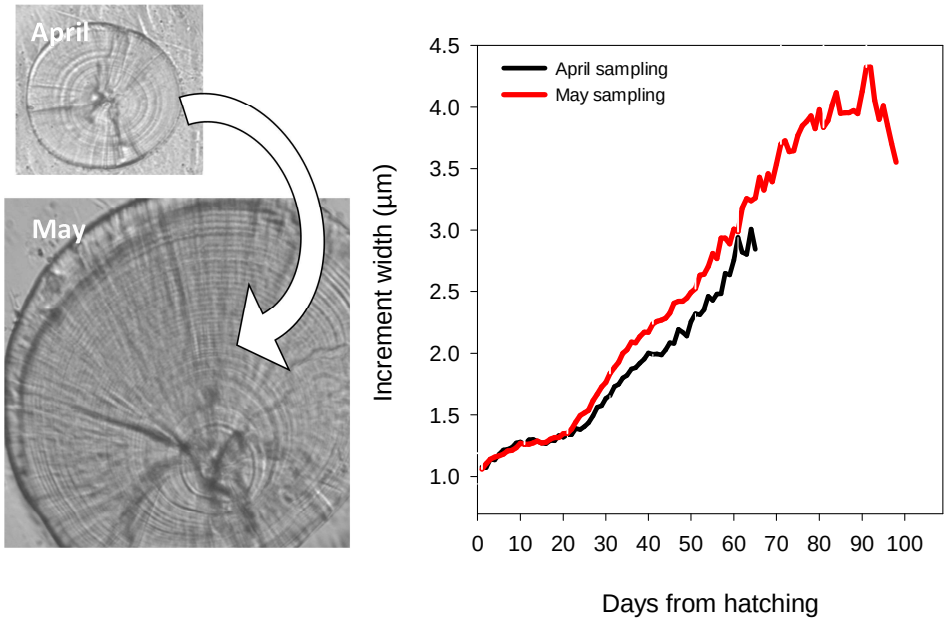


Figure 14. Assessing growth dependent mortality from otolith information.

By following a cohort of larvae by representative sampling in two timeperiods, we investigated whether the surviving group at the second sampling had other growth trajectories up to the first sampling than found for the entire group at the first sampling. Examples of otoliths in larvae from the two periods are illustrated to the left. In April the larvae were at a maximal age of 65 days and the growth trajectories, illustrated by temporal variability in average ring widths, were as the black curve in the figure. In May the larvae were of maximally 105 days of age and we found that the estimates of average ring widths during initial 65 days had increased (red curve). Hence these findings indicate a relatively higher mortality of the slow-growers, while their disappearance could explain such change in the average growth trajectory. From [15].

specimens from the central parts of the distribution. We assumed that we had drawn two representative samples from the same population. The otoliths were dissected, ground and the number and widths of rings were estimated. We then used the widths of rings to evaluate growth trajectories (Fig.14). As mentioned the relation between otolith and somatic growth is influenced by environmental factors, but in our investigation we assumed that larvae were sampled representatively and that they consequently had experienced the same conditions during growth. Thus, we assumed that differences in measured ring widths result from growth rate differences.

The larvae apparently had been hatched over quite a long period, about 60 days, and we distinguished three cohorts each of which had hatched within 20 days. Subsequently, we based on ring widths compared the growth trajectories of a cohort sampled in April with the growth trajectories of the same cohort when sampled in May (Fig. 14). For two of the three cohorts the trajectories differed significantly. The average growth rate of the survivors to May was faster than that of the group sampled in April during comparable days; hence it was mainly slow-growers that had been lost during the intervening period. Thus, the study pointed to growth rate dependent mortality in this cohort of larvae.

A central assumption in the study was a representative sampling of larvae by both surveys. We found support for the larvae being from the same populations from 1) the displacement of distributional centers being in accord with models of prevailing currents in the area, 2) the back calculated times of hatching for larvae assigned to the same cohort were approximately the same and 3) the patterns of growth during the very early stages were similar. Further, we examined the uncertainty of selecting representative stations by examining the consequences of other procedures for choosing stations, and the significance of differences between sampling periods was similar for all procedures.

In order to assess the magnitude of mortality differences among larvae of different growth rates, we used the calculation procedure suggested by Anderson (1995), which estimates the difference in their relative survival probabilities. Using a growth-rate measure derived from the relative size of the otolith at the first sampling date, the calculations showed a big difference. The slowly growing larvae could have experienced up to 10 times the mortality of the fast growers. This is in accord with other analyses showing that even small growth-rate and size differences can lead to great differences in accumulated mortality (Houde 1987, Luecke et al. 1990).

Assessing differential mortality from the diet of a predator, sandeel at Greenland [13].

Another way to evaluate whether the risk of death is greater for smaller members of a population is to assess the risk of being eaten from inspection of stomach contents of predators. Such an investigation was carried out off Greenland, where the distributions of sandeel (*Ammodytes* sp.) and small juvenile stages of two species of wolffish (striped wolffish, *Anarhichas lupus*, and spotted wolffish, (*A. minor*) were surveyed [13]. During earlier investigations off Greenland, the predation of juvenile wolffish on larvae of other fish had been observed, in fact they can be cannibalistic (pers. comm., A. Guzmann).

The investigation took place along a transect of sampling stations off Lille Hellefiske-Banke on the west coast of Greenland. In central parts of this transect the distributions of sandeel and wolffish overlapped. Wolffish (25-45 mm length) and sandeel (15-25 mm length) were sampled in the same net, and later the identifiable items in the wolffish stomachs were counted and measured. Contents included copepods (*Calanus* spp.), amphipods (*Parathemisto abbyssorum*) and sandeel larvae. In both species the diet changed with wolffish size. The smallest of the striped wolffish (<30 mm) fed almost exclusively on copepods and amphipods, but the amount of copepods declined the larger the wolffish became, while the amount of amphipods and sandeel larvae increased significantly. The two wolffish species differed in feeding preferences; at sizes above 35 mm the spotted wolffish ate more copepods and amphipods, while it was mostly the striped wolffish that preyed on the sandeel.

The size of the striped wolffish and the sandeel in its diet were directly related, the relative predator to prey sizes remained roughly constant. This is in accord with the earlier description of relative predator-prey sizes for fish larvae eating copepods, seen in this case for a predator on fish larvae. During growth the predator, here the juvenile wolffish, seeks to satisfy its increasing food demands by inclusion of larger and larger prey.

We compared the stomach contents of the striped wolffish with sizes of sandeel in the immediate environment and calculated size preference using Eq.4. There was much higher preference for the smaller sandeel (<22 mm), (Fig. 15). The preference curve

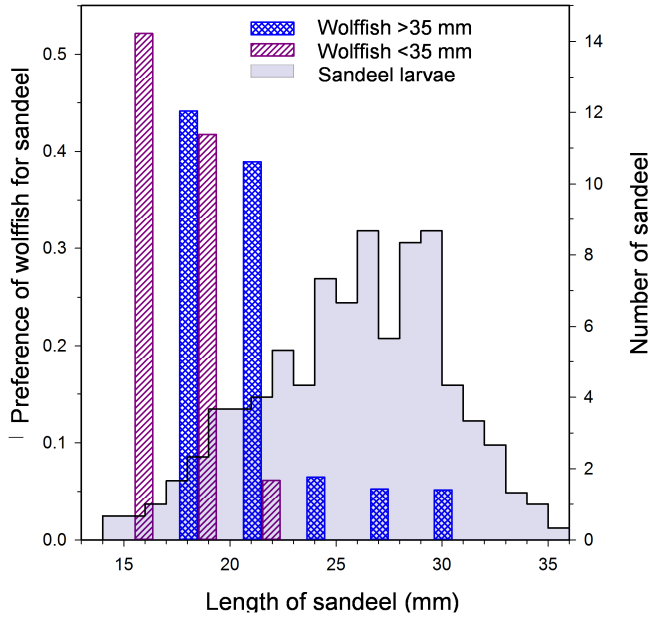


Figure 15. Assessing predation pressure on sandeel larvae.

Based on stomach content analysis the predatory impact of wolffish on sandeel in an area off West-Greenland was estimated. The smallest sandeel were of great importance to wolffish feeding (apparent from preference spectra illustrated by colored bars), and the larger the wolffish the better they could predate the more abundant sandeel in the middle of the sandeel size spectrum (grey bars). Hence, this can be seen as a race between predator and prey toward obtaining high growth rates: the predator would benefit by reaching sizes were it can predate the more abundant sandeel, while the sandeel would benefit by growing "out of reach". From [13].

illustrates the relative predation pressure on the larvae; evidently the predation risk is higher for larvae at the lower end of the size spectrum. Thus, this investigation points to growth rate - and size- related mortality: relatively slower growth can result in a relatively higher risk of being eaten. The findings also illustrate that juvenile fish that have fish larvae on the menu can benefit from a higher growth rate. When small juveniles are present with larvae born the same year, it becomes likely, as seen in this case, that the juveniles would initially prey on the smallest fish larvae in the population, which are relatively less abundant. If they succeed in growing faster than their prey, they will be able to eat progressively larger and more abundant larvae and thereby grow even faster. In this way, there will be a race between the populations of predators and prey, faster growth of the predator results in intake of more and larger prey, while faster growth of the prey lowers its mortality risk.

In addition the observations were used for assessment of the absolute predation pressure (P) on the sandeel population [13]. For this, we used data on the absolute abundance of sandeel in the stomachs of wolffish (MSC), an assumed rate of digestion (D) and the abundance ratio of wolffish to sandeel (R) at the Lille Hellefiske Banke site, as:

$$P = MSC*D*R \qquad \text{Eq. 9}$$

On stations where the wolffish were of relatively high abundance, we calculated P at 0.03-0.05 d^{-1}. This is a mortality of the same order as that estimated for a range of larval fish species (Houde 1997), indicating that in this area the wolffish are important predators and of great influence for the survival of the coexisting sandeel population.

5 SPAWNING AND NURSERY AREAS

As mentioned in the Introduction, spawning and nursery areas apparently possess a set of unique characteristics. Here hydrographical processes lead to enhanced production and generally good conditions for larval growth and survival, but equally important the conditions should ensure retention and optimal drift in order to keep the population assembled and afford possibilities of lifecycle closure (Sinclair 1988, Bakun 2006). In the following I will review a series of specific investigations of the distributions of spawning and nursery areas. Patterns of spawning areas and differences between species are investigated for the North Sea winter/spring spawners (Section 5.1 based on [19]), when the examination of nursery areas covers an extended series of different species in quite different areas, in the West Greenland, North Sea, Sargasso Sea and Andaman Sea (Section 5.2 based on [3, 12, 14, 16, 20, 21] and Munk et al. 2002). The dispersal and drift of larvae are ascertained from repeated surveys on the same cohort of larvae, and from observations of directions of currents in vicinity of larval concentrations. (Section 5.3 based on [2, 3, 5, 20]).

5.1 Spawning areas

The lives of fish take off where the eggs are spawned. Why exactly there, what is behind the spawner's choice of spawning site? This question is vital, and consequently intensely debated. Planque et al. (2007) suggested that for the discussion of the influence of environmental conditions on the choice of spawning sites, it is necessary firstly to define what is meant by a spawning area. Three types of delimitations were suggested: 1) potential spawning areas have suitable conditions for spawning, 2) realized spawning areas are those where spawning actually has been observed by presence of eggs, and 3) successful spawning areas are those from which surviving recruits have developed from the hatched larvae.

Such considerations about the delimitation of spawning areas for the analysis of environmental relationships are taken into account in the interpretation of results from a large international investigation of spawning areas of fishes in the North Sea [19]. During an intensive survey program, eggs and larvae were sampled during a 3 week period in February-March 2004. There was no precedent for such a large survey program during which spawning in the entire North Sea was assessed during the primary spring

Variety of fish egg sizes.

During the investigation of fish spawning areas in the North Sea [20] we found in total 13 different species of eggs. These are relatively easy to identify when alive, while it is much more difficult when they are preserved. Egg size is a helpful measure in the identification. The photo shows small dab eggs (*Limanda limanda*), intermediate sized cod/-whiting eggs, and large plaice eggs. The single egg with a wide space between yolk and shell is a long rough dab (*Hippoglos-soides. platessoides*).

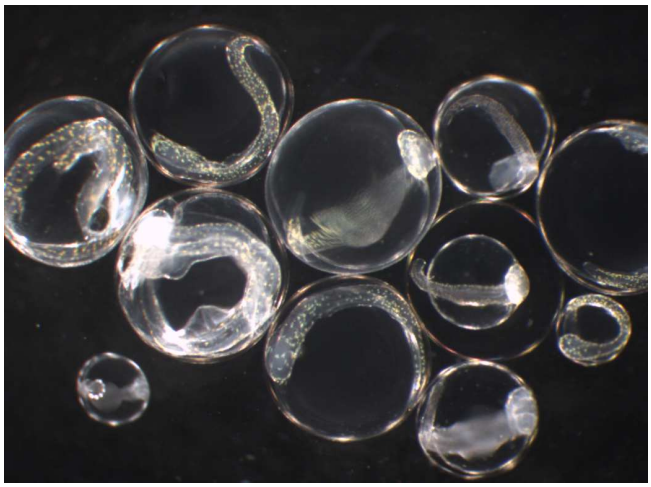


Photo P.Munk

spawning period, and there was an urgent need to update existing, fragmentary information by a full coverage. The survey program had a number of sub-goals, among which were to describe species diversity (Taylor et al. 2007), to specifically delimit the spawning areas of cod (Fox et al. 2008) and to investigate the relationship between egg and larval distributions and the extent of hydrographic fronts [19].

The fronts in the North Sea had been considered in the classical study by Iles and Sinclair (1982) in which they evaluated the importance of tidal fronts for the retention of herring larvae. These tidal fronts are mainly established in the summer/autumn period due to tidal influences on thermally stratified water masses. However, in winter/spring the water column is not yet thermally stratified. During this early period another type of fronts dominates, the estuarine fronts that are related to the freshwater outflow along the coasts. The 2004 study on linkages between spawning and frontal hydrography provided a new angle on these estuarine fronts by covering hydrographic characteristics prevailing during the winter/spring when most of the fishes in the North Sea spawn.

We illustrated how freshwater along the British coast, especially in the southeastern North Sea, generates prominent fronts in areas over 30-40 meters depth (Fig. 16). In the southern North Sea the freshened water masses spread far out to Dogger Bank, covering an area described as the “Regions Of Freshwater Influence” (ROFI) by Simpson et al. (1993). Additionally a prominent front was seen along the Norwegian coast, at the outer edge of the “The Norwegian coastal current” (Mork 1981).

Vertically stratified sampling of fish eggs showed that all eggs were homogeneously distributed at least down to 35 m, which was the deepest sampling depth. Horizontally

the eggs were often concentrated in specific areas along the frontal zone, while egg concentration was relatively low in other areas. Apparently most spawning activity took place in vicinity of fronts, but each species spawned in restricted sections of these (Fig. 16). In a comparison to historical information on spawning intensity, we found that for cod, for which a quite long record on spawning activity is available (e.g. Brander 1994), some of the historical spawning areas were not included in the 2004 spawning. Most species, however, showed a high degree of reappearance in certain geographic areas, and most potential areas of spawning were apparently still in use.

Spawning is seemingly much restricted in time and space. Fish seek areas with specific characteristics to release and fertilize their eggs, and their choice appears to be a compromise between geographical 'stability' and adaptation to hydrographic characteristics. The geographic factor could be recognizable physical characteristics, which would be an obvious driver for demersal spawners who are dependent on appropriate

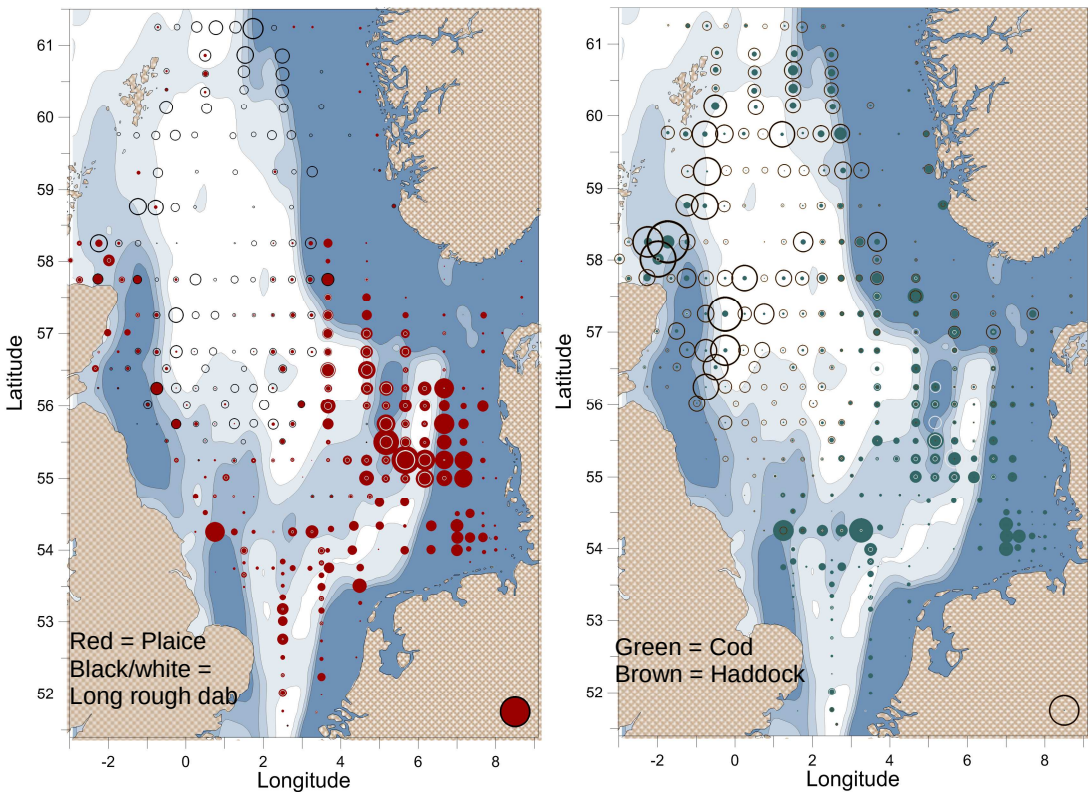


Figure 16. Spawning areas of fishes in the North Sea assessed by abundances of eggs.

Illustration is based on an international survey of eggs in February-March 2004. Abundances of egg from four species, cod, haddock, plaice and long rough dab, are illustrated by size of circles, and these are imposed onto a contour map of horizontal change in water density at the surface. The intermediate level (light blue) indicates the interface between water masses, i.e. frontal zones. Areas of spawning differed between species, however all the more prominent egg concentrations were in vicinity of the estuarine fronts prevailing during the investigated period. From [19].

substrate for their eggs. But spawners also appear to orient themselves to hydrographical characteristics. This is supported by the observations of species reappearing at the same positions relative to hydrographical frontal zones, even when habitats are geographically very close [19]. It is still unknown what cues fish use in their movement toward and identification of their spawning areas; it can be specific physical/chemical combinations, possibly including a specific scent from a given area as seen for salmon (Hasler & Scholz 2012).

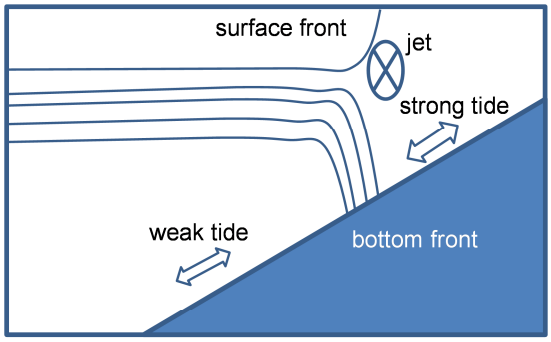
5.2 Nursery areas

The position of spawning areas is not only determined by the immediate characteristics of the site. In an evolutionary context the position would also be determined by the possibilities for the following larval life, for example whether the area offers optimal drift and growth conditions for larvae and ultimately results in a high survival probability. Thus, insight into the larval fish ecology both lead back toward a greater understanding of spawning strategies and forward toward understanding of fish life-cycle closure and recruitment to the stock.

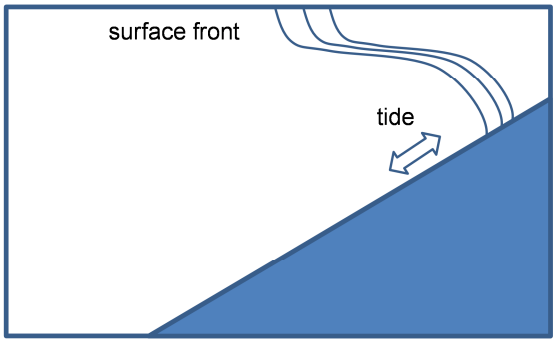
The distributions and ecology of fish larvae have been described in a long series of studies, illustrating the great variation in the lives of fish larvae. The numerous species of fishes have adapted to (almost) all aquatic environments. Therefore, we see varied adaptations during all stages of a fish's life, and we find fish larvae growing in environments from small ponds to the great ocean. In the marine environment opportunities and adaptation will differ markedly depending upon the given habitat, whether it is e.g. coral reef fishes, fishes living at sandy bottom or fishes from the open sea. It is well recognized that universal characteristics of fish nursery areas relate to hydrographic patterns and processes. It is not within the scope of this thesis to cover all possible adaptations and physical linkages in the early life, the focus here is on the nursery areas in the open sea and the related hydrographic phenomena here – particularly on the hydrographic fronts, which shape marine ecosystems across the globe (Belkin et al. 2009).

Aiming to check and characterize a potential universal importance of fronts for the early life of fish, I have carried out a series of studies covering a range of species, seasons and climate zones. The nursery areas of fishes were the primary focus, but the work also came to be strongly oriented toward understanding frontal hydrography and the (other) bio-physical linkages related to these. In the following I will describe and compare those studies, illustrating the conditions for different species, for different types of fronts and for different climates. I will refer to four important types of fronts, these are described and illustrated in Fig. 17.

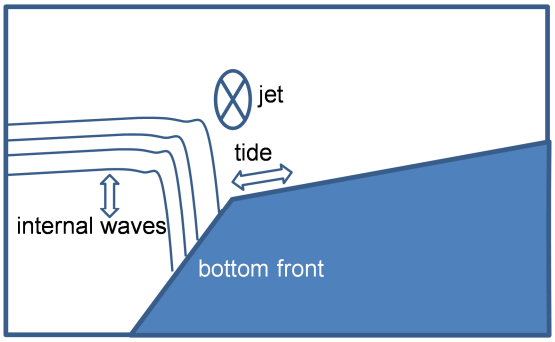
a) TIDAL MIXING FRONT



b) HALINE / ESTUARINE FRONT



c) SHELF BREAK FRONT



d) OCEANIC / SUBDUCTION FRONT

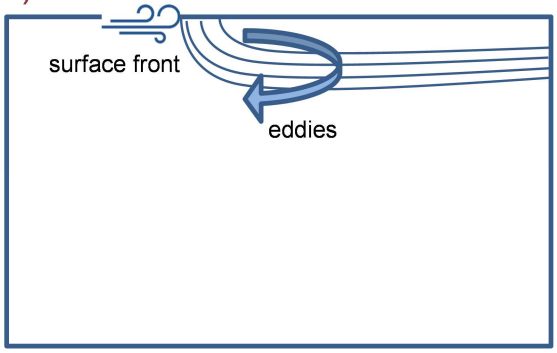


Figure 17. Schematic illustration of four types of hydrographic fronts.

Fronts of importance for the early life of fish. Contour lines indicate changes between water masses of different density, either dominated by temperature or by salinity differences.

a) The tidal mixing front is mainly seen inbetween temperature stratified water and water mixed by strong tidal excursions. It dominates in summer/autumn when solar heating leads to temperature increase in surface water. Isohalines will to some extent follow the isotherms.

b) The haline or estuarine front is found where fresher water from river outflow meets the more saline offshore waters. The relatively fresh water will flow above the saltier, and due to mixing processes both at surface and at bottom relatively sharp fronts will be established there.

c) As the name indicates, shelf break fronts are found where there is a sharp increase in bottom depth at the shelf break. At these depths there is often an influence from internal waves, which are long wave undulations of the deep pycnocline mainly generated by tidal energy. The undulations and tidal excursions at the slope lead to mixing and establishment of a front.

d) Oceanic fronts are often seen when heavier cold water subducts below warmer water masses in oceanic regions. They are generated by solar heating and windstress. Currents and eddies create strong mixing at the interface between water masses, leading to a complex frontal zone.

Herring in the North Sea - tidal (mixing) fronts [3]

In earlier sections I have mentioned projects based on field investigations of the autumn spawning herring off the coast of Scotland. These investigations were carried out in the period 1983-1988 and focused on the distribution and life of herring larvae in relation to hydrography and feeding conditions [2, 3, 4, 5]. All surveys of larval distribution were carried out along cross-frontal sampling transects, and we could show a strong relationship between larval distributions and specific characteristics of the tidal front. This was the case both for the position of the spawning sites, determined as the initial location where newly hatched larvae were seen in very high concentrations, and for the full extent of the nursery areas, as determined by the distributional areas of larvae during development.

The fronts off Scotland are established at the interface between tidally mixed and thermally stratified water masses (Fig. 17a). In a classical description of this type of front Simpson (1981) used a measure of the stability of the water column, expressing the amount of energy that would be needed to mix the water column to vertical homogeneity. This stratification parameter is calculated from:

$$\phi = g\, h \int (p - p_o)\, z\, dz \qquad \text{Eq. 10}$$

where g is gravity, h is bottom depth, p is water density at depth, p_o is the density average for the entire column, and z is depth. The unit becomes J m^{-3}.

The stratification parameter is near zero in the tidally mixed water, rises across the front and reaches a high stable level where the water column becomes fully stratified. The frontal zone is then defined as the area where ϕ shifts from zero to its maximum value, which off Scotland was around 80 J m^{-3}. We found the largest amount of newly hatched larvae - and thereby an indication of the positions of spawning areas - just within the frontal zone at the inshore side where $0 < \phi < 30$ J m^{-3} (Richardson et al. 1986, [3]). The strong tidal excursions at the inshore side of the front, and the jet current established above the bottom under the front (Hill et al. 2008), have the consequence that the finer sediments do not settle to the bottom in these areas. This results in bottom sediments mostly of stones and gravel. These conditions are ideal for the demersal spawning of herring, which needs a stable substrate for the eggs, combined with currents exchanging water around the eggs.

Using parallel sampling of herring larvae and their potential prey, primarily copepods, we investigated whether the larvae were distributed in areas of especially favorable feeding conditions. There were generally no changes in the estimated biomass of copepods across the frontal zone, while their productivity peaked at the offshore side of the frontal zone. Abundances of herring larvae peaked in central areas of the frontal

zone, and we could not prove a direct relationship between larval abundance and copepod biomass or productivity. Actually, we found indications of a reverse relationship between larval abundance and biomass of the copepods less than 200 µm body length. The probability that this inverse relationship could be due to predation pressure by the larvae was treated in section 4.3. Another cause of the inability to prove direct linkages between larvae and their prey could be inadequate assessment of the available prey biomass. As discussed in section 3.2, only a fraction of the total biomass of copepods would likely be available to the larvae, and the used assumption that all copepods <200µm would be equally preferred and equally available could be invalid.

Plaice and sandeel in the North Sea - estuarine fronts (Munk et al. 2002)

As described in section 5.1 prominent estuarine fronts (Fig. 17b) are established in early spring in the North Sea. The investigation carried out in late February showed enhanced abundances of fish eggs in these frontal areas [19], while an investigation carried out in late March, provide the opportunity to evaluate conditions when eggs have hatched into larvae (Munk et al. 2002). This study generally found larval distributions limited by the estuarine fronts; for cod and plaice the important areas of distribution were at fronts in the areas of German Bight, Horns reef and Dogger Bank, while sandeel distributions were related to fronts off the coast of Yorkshire.

Water density variation during early spring in the North Sea is mainly determined by salinity. The marked gradient in water density characterizing the coastal fronts is based on those salinity differences. We used a specific water density measured at the surface, 1027.35 kg m^{-3}, as an indicator of the central areas of the coastal fronts, and we estimated that as much as 87% of all larvae were shoreward of this limit (Munk et al. 2002). Within this area the highest densities of plaice (*Pleuronectes platessa*), sandeel and cod larvae were found in the band along the front where the horizontal density gradient in surface water was greatest.

Estuarine and thermally based tidal fronts are often intermixed (Simpson et al. 1993). During spring thermal fronts increase in strength and importance, and during that period we observe stronger spatial differentiation of the different species of fish larvae. During their later larval stages plaice will be distributed more southerly and inshore in the North Sea, linked to the estuarine fronts, and they settle later in the Wadden Sea (Bergman et al. 1989), while sandeel and cod larvae will be distributed in more northerly areas where other types of fronts prevail [12].

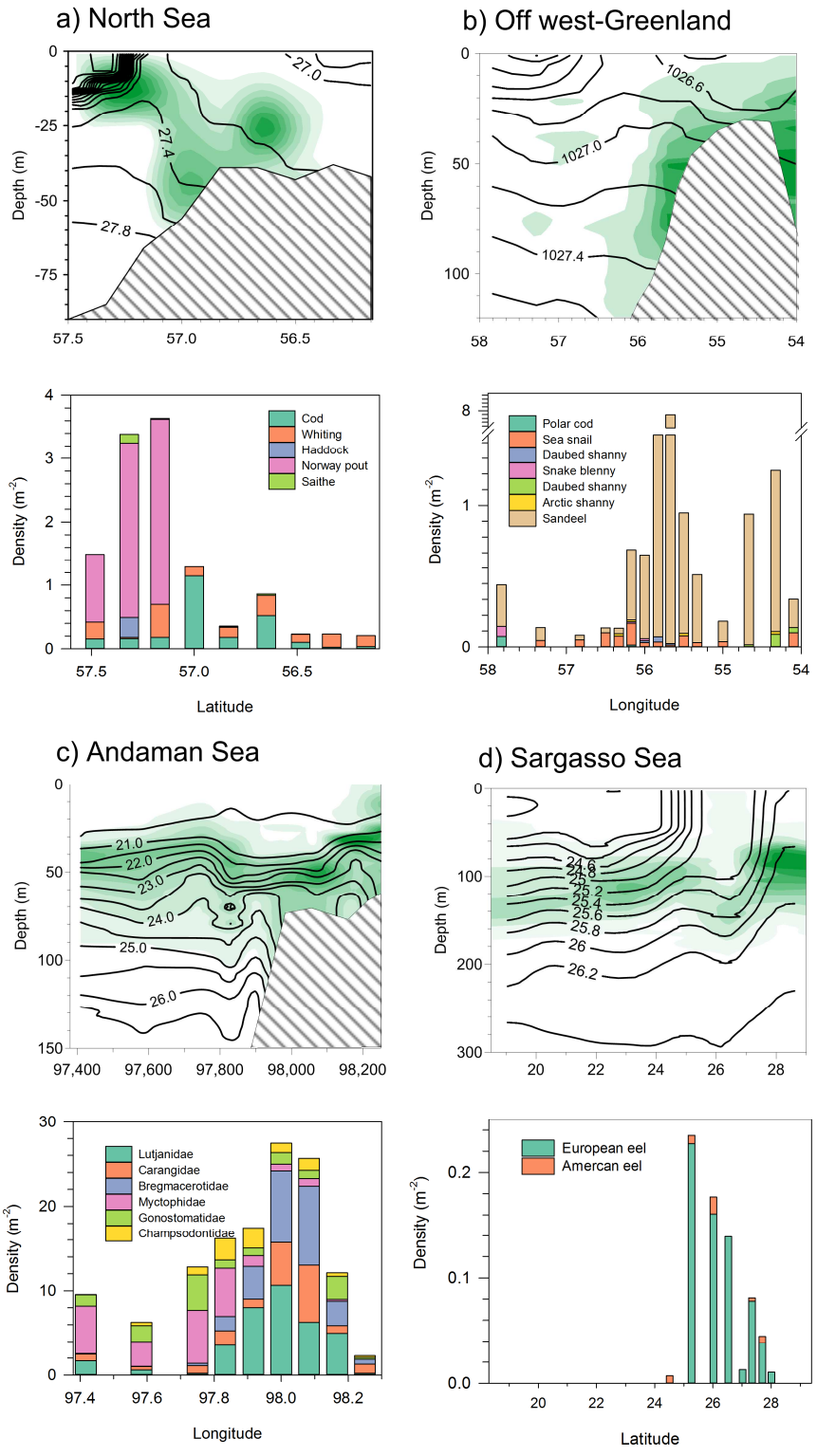


Figure 18. Observations along cross-frontal transects in four different climatic zones.

Upper graphs show vertical sections of water density (by contours of sigma-t, kg m^{-3}) and algal abundance by their fluorescence (by different green shading). Lower graphs show the abundances of fish larvae for the more numerous taxa at site (by stacked bars). a) Temperate area in the North Sea (off Hanstholm, west Denmark), b) Subarctic area off west Greenland (Store Hellefiske Banke), c) Tropic area in the Andaman Sea (off the west coast of Phuket, Thailand) and d) Sub-tropic area in the Sargasso Sea. From [12, 14, 16, 20].

Gadoid larvae in the North Sea - estuarine and shelf-break fronts [12, 21]

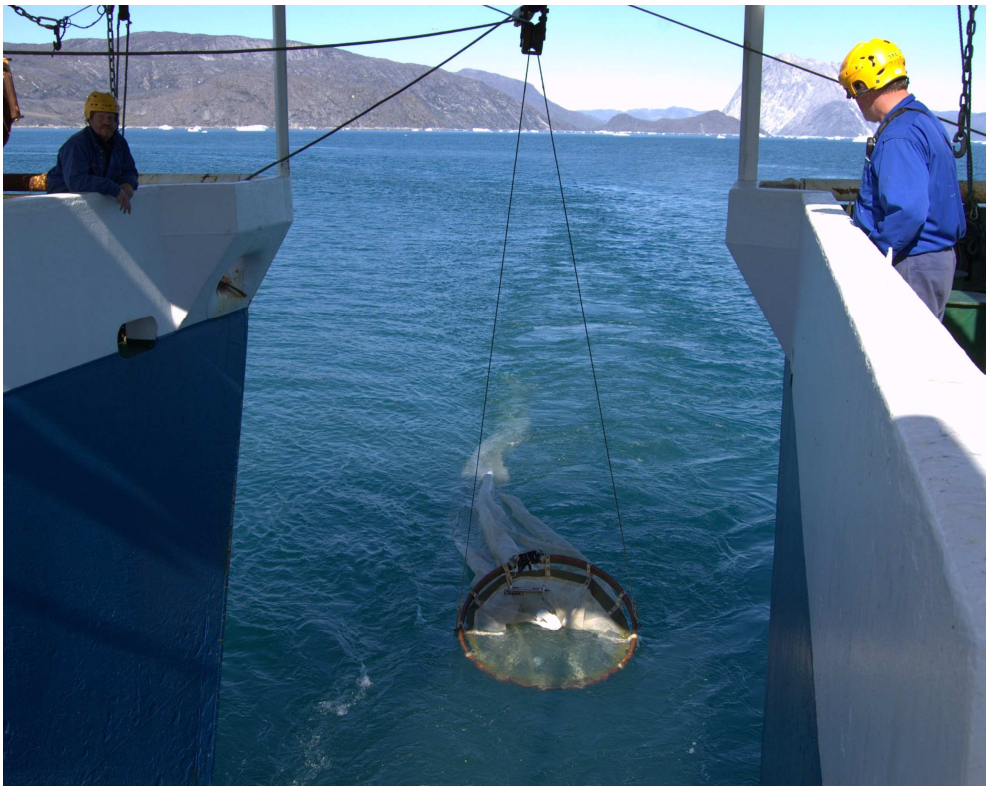
A variety of gadoid fish larvae depend on fronts in the northeastern North Sea as nursery areas [12, 21]. In this area several water masses of different origins and character meet, and the area has very complex hydrography. The Jutland Coastal Current, Central North Sea Water, Atlantic Deep Water and the Norwegian Coastal Current are all present, and, depending on water depth and the converging water masses, different fronts are established. Fronts related to the fresher coastal currents are of estuarine character, while the front between Central North Sea water and Atlantic Deep Water has characteristics of a shelf-break front (see Fig. 17b,17c, 18a).

During investigations of gadoid larvae across these fronts, we observed marked shifts in larval fish abundances and species composition. Investigations were carried out during 1991-94 and 1997 and included the closely related species whiting, cod, haddock, saithe and Norway pout [12, 21]. The area of investigation extended from the northeastern North Sea, through the Skagerrak and into the Kattegat, and sampling was primarily carried out along transects from shallower areas toward deeper areas, planned so as to cross one or more fronts.

While the absolute abundances of the larval species showed marked fluctuations from year to year, there were common patterns in larval distributions. All the species were distributed in and along the frontal zones, and generally all the abundances were low at the most inshore and most offshore stations, while they peaked somewhere in the frontal zone. These peaks were often seen at the station positioned at the defined center of the front, but, when inspecting all sampling sequences across all years, a definite species-specific pattern of peak displacement was evident. [12]. When this horizontal pattern was resolved vertically across the frontal zone, we saw some vertical separation of species in sections with horizontal overlap ([21], Fig. 6). The order of the species in their horizontal distributions (from inshore to offshore) (Fig. 18a) agreed well with the order downward in the water column (Fig. 6), indicating that the distribution and separation between species are determined by specific physical/chemical gradients common to the pycnocline and frontal zone. Water masses in the pycnocline and front are connected, and the front is a zone of both horizontal and the vertical gradients. Apparently, the distributions of larvae followed physical/chemical variations horizontally across the front, as well as in the vertical dimension [21].

We carried out parallel studies of the abundance of preferred prey organisms on a cross-frontal scale and on a combined horizontal-vertical scale. In the latter case we examined the spatial correlations between the different species of gadoid larvae and copepods. Less than 30% of the correlations were significant (at $p<0.05$), and several of these were negative, pointing out the large species-specific differences between distributions both

in horizontal and vertical dimensions. These differences will lead to differences in the amounts and composition of prey available to the species of larvae.



Retrieval of the 2 meter ring net (MIK) onboard r/v DANA at Greenland

The 2 meter ring net (MIK) was the most used gear for sampling of fish larvae, launched in both the sub-arctic Greenland, the North Sea and the tropical Andaman sea. The relatively large gear opening (relative to fish larvae, not to the size of DANA!) was used in order to better catch the larger sized larvae, which is not appropriately sampled by the smaller, traditional gears, as for example the Bongo nets. The net of the MIK is in this case white monofil net, in other cases black, woven nets were used. Examples of net types are illustrated in the book for identification of North Sea larvae by Munk and Nielsen (2005). Photo P. Munk.

Fish larvae in sub-arctic Greenland – shelf- break front [14]

Field investigations at West-Greenland in the summer of 1996 provided an opportunity to examine the importance of hydrographic fronts for the life of fish larvae in arctic and sub-arctic conditions [14]. During these investigations we measured physics and chemistry and sampled zooplankton along transects, from shallow coastal areas to the deeper waters offshore, and from the arctic/sub-arctic Disko Bay to boreal marine areas

off Nuuk. All transects crossed the important fishing banks off the western coast of Greenland, and fronts related to the prevailing currents were apparent in the entire area of investigation (Figs 17c, 18b). South of Disko Bay these fronts occurred at the shelf break at depths of 80-90 m between the West Greenland Current inshore and the colder Polar current. During later investigations (Simonsen et al. 2006), we noticed prominent undulations of the pycnocline, and measured breaking internal waves reaching amplitudes up to 8 m (C. Stenberg, pers. comm.). Internal waves are long undulations of the pycnocline created by tide or wind. They are spread over great distances and are amplified at the shelf break, releasing energy by turbulence and mixing. This is of importance to the upwelling of nutrients and the front establishment at these sites (Pingree & Griffiths 1978, Helfrich & Melville 1986). Thus our study pointed out the importance of internal waves for frontal hydrography at the fishing banks off West Greenland.

At the fishing banks off West-Greenland we observed enhanced nutrient concentrations at shallow depths produced by the upwelling. While nutrients entrained from deeper waters will be quickly assimilated in primary production, our observations suggest strong mixing in the area. Accordingly, we found enhanced algal abundance in the frontal zone while the abundance of copepods showed no unambiguous relationship to the positions of fronts. However, distributions of copepod species differed markedly.

The nursery areas of fish larvae in this area of investigation generally coincided with frontal zones, but differences among species were apparent across fronts and along the north/south axis. In the boreal areas, represented by the two southernmost transects over the Sukkertop Banke and Fyllas Banke, the dominating species were Arctic shanny (*Stichaeus punctatus),* Greenland halibut (*Reinhardtius hippoglossoides*), long rough dab (*Hippoglossoides platessoides*) and sandeel (*Ammodytes* sp.). Of these the Arctic shanny and sandeel were the more coastally distributed, while long rough dab and Greenland halibut were located more offshore. In the arctic/subarctic area, along the transect crossing Disko Bay and Disko Bank, it was the more arctic species, including polar cod (*Boreogadus saida*) and striped sea snail (*Liparis* sp.), that were found in central areas of the fronts. Of those two, the sea snails were located more offshore, mainly at Disko Bank, while polar cod were primarily found in the bay close to the skerry areas at its entrance. These observations of fronts and fish larvae at Disko Bay have been verified in a more recent examination of assembled 1997 data, showing the same distributional patterns of larval fish species, but in much different abundances (Munk et al. 2015).

Our observations of larval fish assemblages agree with observations from standard-cruises carried out off Greenland in the period 1925-84 (Pedersen and Smidt 2000). In

their analysis of the historical data series, Pedersen and Rice (2002) pointed out a range of important, species-specific characteristics of the fish larvae investigated. Their demonstration of the influences of salinity and water depth are in accord with our results on fish larvae and fronts in the same area [14]. During that historical period, larval cod (*Gadus morhua*) were found across large parts of our investigated area as well, but this species gradually disappeared from the traditional nursery areas off the fishing banks from the late 1980's onward

Fish larvae in the tropical Andaman Sea – tidal mixing and shelf-break fronts, internal waves [16]

During a cooperative research program between Thailand and Denmark in 1996-2000, we carried out an intensive study of the planktonic ecosystem off the west coast of Thailand. The objectives were to gain information on the hydrography and primary productivity in the area and to assess environmental influences on larval fish nursery areas (Nielsen et al. 2004, [16]). The Andaman Sea is renowned for the influence of huge internal waves in the pycnocline. Well out to sea, internal waves have long wavelengths and small amplitude, but at approximately 300 m bottom depth the amplitude increases substantially, leading to strong mixing and intrusion of nutrients that potentially enhances primary productivity. Farther inshore at 50-60 m bottom depth, the upper pycnocline reaches the bottom, and further mixing processes lead to establishment of a front between inshore mixed and offshore stratified water masses (Figs. 17a, 17c, 18c). Our working hypothesis was that this characteristic hydrography would determine the overall productivity and be a decisive influence on distributions and composition of larval fish assemblages in the area. Further, we expected the seasonal monsoon in the area to influence both hydrography and productivity at all trophic levels, so surveys were planned to cover two different monsoon periods.

The prominent internal waves in the area have their basis in the strong pycnocline that is due to intense, tropical solar radiation and thus temperature stratification, and due to the geographic layout of the Andaman Sea characterized by shallow passages between a series of islands at its western limit. Tidal excursions over these shallows lead to undulations in the pycnocline, and a set of about eight so-called solitons are produced according to the tidal cycle, i.e. every 12.4 hour. This original set of solitons leads to further undulations of the pycnocline, and at the shelf we observed continuous propagation of internal waves, though with intervals of special intensity. It was fascinating to follow the propagation of the internal waves. Due to the enormous amplitude of the waves (up to 65 m), they were clearly visible at the surface as repeated patterns of 'oily slicks' and 'ripples'. When we launched the CTD, the rising wave could be of such intensity that the instrument would almost refuse to descend in the water column.

In the tropics there is a great number of larval fish species, and accordingly several hundred fish species were found during our investigations in the Andaman Sea. We identified to family-level only, and that included up to 109 different families. Thirty five of those families were sufficiently abundant to exhibit distributional patterns and peaks of abundance. A cluster analysis looking at the relationship between stations and based on relative proportions of families showed significant structuring of the larval fish community. This familial structuring of the larval community was especially apparent in the inshore-offshore direction. Most prominently, the assemblages were separated across the shelf, and inshore of the break a close-to-coast assemblage was distinctly separate from the other larvae (Fig. 18c). The along-coast differences were less significant.

In addition, the absolute abundances of larvae were structured from the coast to seaward. Abundances peaked in the frontal areas at 50-60 m depth, offshore the shelf break and in the area where internal waves were amplified. On the lower trophic levels we could not show significant relationships between biomass and hydrographic (front-) characteristics, probably due to the high turnover rates in tropical marine areas (Nielsen et al. 2004). But our results indicate a linkage between distributional patterns of larvae and hydrographic characteristics. Larval abundances might 'integrate' processes taking place at lower trophic levels for a prolonged period and thereby be better indicators of the bio-physical linkages in the area.

Eel larvae in the subtropical Sargasso Sea –oceanic fronts [20]

During the Danish Galathea III expedition of 2006-2007, we were provided the opportunity to investigate the early life of eels on the shared spawning grounds in the Sargasso Sea of American eel (*Anguilla rostrata*) and European eel (*Anguilla anguilla*). Since the 1980's, recruitment to eel populations has shown a dramatic decline, for European eel to only 2-5% of its former size, and this research initiative was motivated by the need for improved understanding of potential climate influences on the early life of eels.

The Atlantic eels spawn in areas of the deep ocean 800 kilometers from land, 6000 km from the European Continent. The life cycle of the European eel has fascinated Europeans since the time of Aristotele, while a naturally spawning eel has never been seen. In the early 1900's the spawning areas of European eel were discovered by Danish marine scientist, Johannes Schmidt. His intensive search revealed that the eel spawns in the Sargasso Sea, far away from the European foraging areas of the adults (Schmidt, 1923). Since the famous investigations by Schmidt, there have been several expeditions to the area (Miller et al. 2014) providing further understanding of the distribution and early life characteristics of eel larvae. Results of this research point to a strong connection between distributions of eel larvae and the location of the "Subtropical Convergence

Zone" (STCZ), where warm subtropical waters meet colder mid-Atlantic water masses (McCleave 1993).

Since this importance of the STCZ for the eel spawning was discovered in the 1980's there have been significant advances in satellite-based observations of sea surface characteristics. There has also been great improvement of our understanding of oceanic fronts in the Atlantic Ocean, including the STCZ and the complex frontal structure in its area (Fig. 17d, 18d, 19) (Ullmann et al 2007). Hence, during our investigation in 2007, we were able to put greater focus on the significance of those oceanic fronts to characteristics of the eel larvae, by using satellite-based surface temperature information to guide our sampling and analysis of results [20]. Our working hypothesis was that the oceanic fronts in the Sargasso Sea basically would be as important to fish early life as observed for fish in the shelf and coastal areas: fronts would provide a range of habitats for different species of larvae, ensure retention of larvae within those habitats, provide (relatively) enhanced primary and secondary production and finally ensure a predictable larval drift.

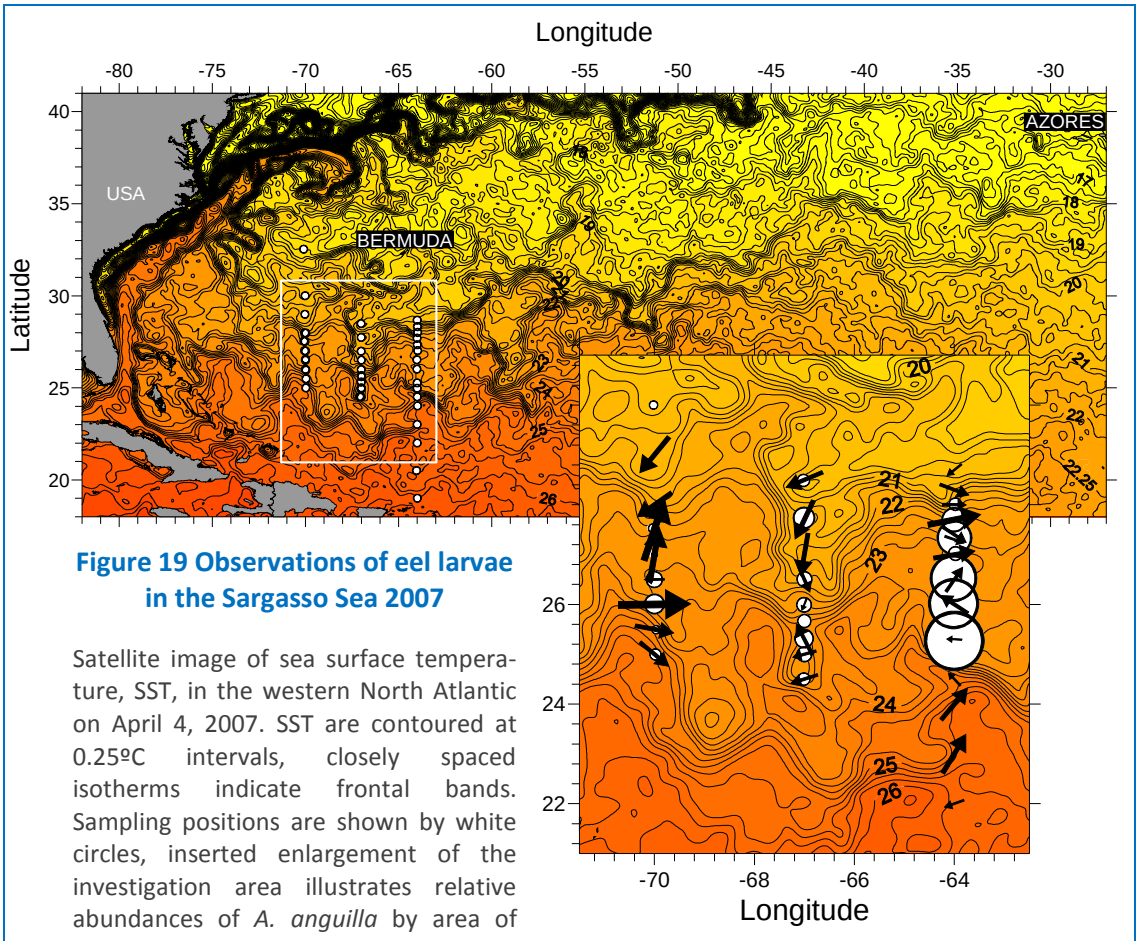


Figure 19 Observations of eel larvae in the Sargasso Sea 2007

Satellite image of sea surface temperature, SST, in the western North Atlantic on April 4, 2007. SST are contoured at 0.25ºC intervals, closely spaced isotherms indicate frontal bands. Sampling positions are shown by white circles, inserted enlargement of the investigation area illustrates relative abundances of *A. anguilla* by area of circles and currents at 50 m depth by size and direction of arrows. From [20]

Abundances of American and European eel larvae sampled along three transect crossing the STCZ were analyzed for their linkage to front and eddy performance in the area. The results pointed to eel larva distributions being delimited within a zone between two prominent fronts, which were apparent from observations of isotherms rising from the thermocline at 100-150 m to the surface (Fig..18d). Dimensions of the total nursery area of eels are of much greater magnitude than seen for other fish larvae; eel larvae can be spread across an area extending up to 400 km across the STCZ and for about 1500 km along the zone (observations in 2014, P. Munk unpubl.).

The STCZ is of complex hydrography, strongly influenced by eddy formation, and accordingly the distributional patterns of eel larvae were complex and patchy. The fish diversity in the STCZ is high and other fish larval species showed linkages to the frontal hydrography as well (Ayala et al 2015). Generally the STCZ showed higher abundances of plankton than seen for neighboring areas (Andersen et al. 2011) and this indicate that this area offers superior feeding conditions to the eel larvae. Findings from stomach contents of sampled eel larvae, analyzed by genetic methods, suggest a mixed diet of eel larvae apparently dominated by marine snow particles and gelatinous plankton (Riemann et al. 2010). Such food demands might best be satisfied in the inter-front zone.

Studies of larval vertical distribution, carried out during a subsequent survey in 2014 showed eel larvae to be highly concentrated during daytime at about 150 m (P. Munk, unpubl.). This was the depth of the thermocline where enhanced plankton abundances were also seen, thus further examination of food-chain linkages of importance to eel larvae should incorporate this vertical variability.

Conclusion on nursery areas and frontal zones.

In spite of differences in origin of frontal features and their dominating processes, we found in all cross-frontal passages the same pattern in fish larval distribution. Abundance of larvae of given species peaked at some point of the frontal zone, and the more central in the zone (were horizontal stratification was at its highest) the more species were present.

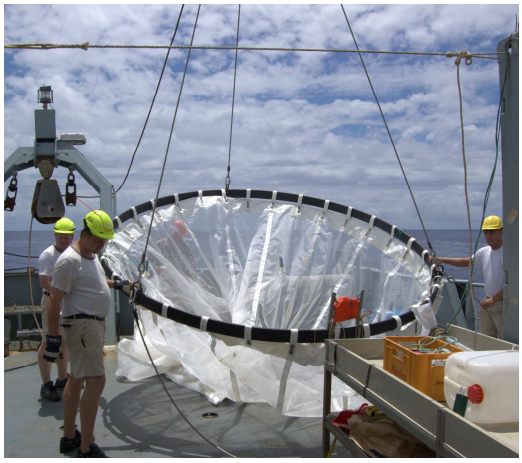
The linkage between peaking larval abundance and fronts (hydrographic transition areas) appears exclusive in the sense that we did not find comparable high abundances of larvae in areas that did not show some frontal pattern, and we did not find a front which did not sustain concentrations of fish larvae.

When acknowledging these commonalities, it was also evident that the fish larval lives differed significantly, obviously the plankton composition and abundances at all trophic levels differed much between the eutrophic parts of the North Sea and the oligotrophic Sargasso Sea, as well as between the sub-arctic Greenland and the tropic Andaman Sea.

These differences are of great use in the comparisons between areas providing abilities to mark out leading processes and mechanisms.

Extra large ring net for catching eel larvae during the Sargasso Sea Expedition 2007.

To ensure sampling of sufficient amounts of eel larvae for analysis, we constructed a ring net of 3.5 meter diameter. This could filter around 36000 m^3 during the oblique hauls we planned to 250 m. Even these huge amounts of water filtered only gave a maximum of 30 larvae in one haul, and larval numbers were mostly much less.



5.3 Dispersion and drift

The question about the degree of dispersion and drift is of fundamental importance to the interpretation and understanding of the influence of fronts and other hydrographic phenomena to the life of fish larvae and their ability to close the lifecycle. In the following I will describe studies where special emphasis has been given to the dispersion and drift of larvae.

Dispersion of herring larvae [2]

In the early 1980's herring were reestablishing spawning in the area off Buchan after the dramatic decline in spawning and stock in the late 1970's. Therefore, relatively few spawning sites were in use then. Especially during our first survey in 1983 we observed only few and separate sites. That provided us with a unique possibility to explicitly measure dispersion and drift [2].

The dispersal of eggs and larvae from a given point source will be determined by a range of factors and processes. In our analysis we used a simple model, assuming that larvae disperse from point sources and that there are both horizontal homogeneity and vertical isotropy. Given these premises the dispersal would follow a Gaussian distribution in all directions (Nihoul 1975). However, dispersion is mainly due to eddy diffusivity and shear from currents. Due to the influence from shear in the direction of maximal tidal velocity the distribution would actually be elliptical. The directional variance of

the Gaussian distribution can be used to express the diffusion by the lateral coefficient of diffusion (K) and the shear (Nihoul 1975):

$K = q^2/2t$ Eq. 11

$Shear = ((3q_a^2/q_b^2)^{0.5})/t$ Eq. 12

Where q^2 is the variance in the given direction, q_a^2 and q_b^2 along the shortest and longest axis, respectively, and t is the time from start of dispersal.

Larval length distributions from the area indicated that three cohorts of larvae had hatched at different times, and we separated them by fitting three Gaussian distributions to length data [2]. Following this, we interpolated the spatial distribution of each cohort using the two-dimensional Gaussian distribution based on the diffusion and shear equations (Eq. 11 and 12). The average diffusion coefficients calculated from three coverages of one of the cohorts showed a clear difference between the cross-front dispersion (34 $m^2 s^{-1}$) and the along-front (213 $m^2 s^{-1}$). A substantial shear (2.3 10^6 s^{-1}) was seen in the frontal zone, probably due to tidal excursions and the jet-current of the front. The diffusion coefficient across the front is in the lower range compared to coefficient calculations in the North Sea in general (50-200 $m^2 s^{-1}$, Okubo 1971), indicating that specific characteristics of the front lead to less dispersal of larvae across the zone than seen for unconstrained dispersion.

Wind effects and tidal excursions lead to some dispersal in the cross-front direction (Chen et al. 2003), but that could be counterbalanced by other mechanisms which lower the dispersion of larvae. A potentially aggregating process is related to the convergence of currents toward the central jet-current of the front. The jet-current is primarily driven by water density differences (Hill et al. 2008) that direct surface currents inward. The inward movement at the surface is counterbalanced by outward currents at the bottom (Lwiza et al. 1991).The intensity of these currents changes during the tidal cycle, and, as mentioned in the description of larval vertical migrations (section 2.5), the vertical displacement might lead to their aggregation and retention (Fortier and Leggett 1983). A migration synchronized to the cycles of the tide and the sun could affect the dispersion of larvae and could be part of a strategy for retention and/or directed advection (Robins et al. 2013).

Drift of herring larvae [2, 3, 5]

During the research program on herring spawning areas off Buchan, we determined the speed of larval drift. In the first weeks after hatching the cohorts could be delimited, and for the year classes of 1983-85 we determined the movement of patch centers, either by use of Gaussian distributions [2] or by use of centers defined from stations of maximal

densities [3], Fig. 20. The estimates of direction and speed of drift were of the same magnitude for all cohorts and years and were about 2-4 km d^{-1} in a southeasterly direction. That is the direction parallel to the front, and the data indicated that the cohorts positioned in the very central parts of the frontal zone, where the jet-current

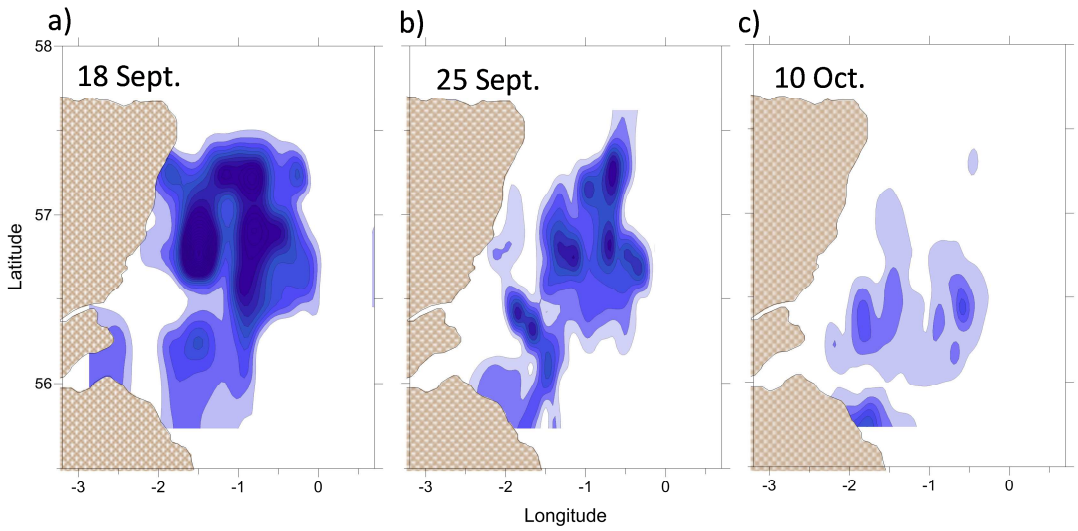


Figure 20 Movement of herring larvae patches at spawning grounds off Buchan

During consecutive surveys the dispersal and drift of herring larvae were followed during the fall of 1985. Intensity of shading illustrates relative abundance of herring larvae during surveys a) to c). Cohorts hatched from specific spawning sites were apparent both in (patchy) distributional patterns and length distributions, and separate drift trajectories were estimated for cohorts. From [3].

probably was located, drifted at the highest speed. In a later study of the 1987 year class [5], we followed the distribution of larvae during the months from spawning until February and analyzed their drift by hydrographic modelling (Bartch et al. 1989). In this model the 'particles' underwent active vertical movements based on observations of the larval herring vertical migrations for the year class [5]. Both observations and modelling showed that the cohorts from spawning areas off Buchan became more mixed, and also that larvae from this and other larger spawning regions, such as those off Orkney/Shetland or off Yorkshire, differed in their respective drift patterns.

The model study pointed to the determining role of larval vertical distribution and migrations for their drift, because different inputs to the model in respect to migration had strong effects on its output, and those virtual migrations could be given a close resemblance to the actual observations. Further, the study indicated that currents and their influence on larval drift could matter greatly to larval survival and subsequent recruitment. In the autumn and winter of 1987/88 the general weather conditions were

quite unusual, slowing the circulation in the North Sea and reducing opportunities for larvae to reach their traditional winter/spring nursery areas in the eastern sector. The year class in question (1987) was shown later to be one of the poorest in many years.

Drift of eel larvae [20]

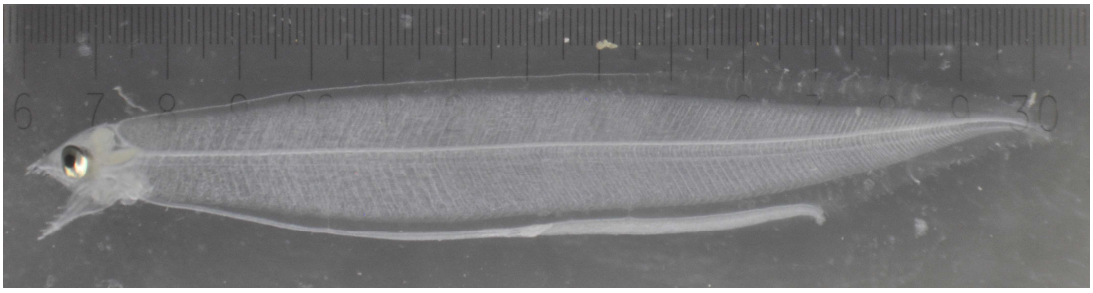
While the understanding of hydrographic processes in relation to tidally influenced, coastal fronts has been greatly advanced and models of fish larval dispersal and drift in these areas have been improved, our knowledge of processes related to oceanic fronts is much more limited. The increasing amount and quality of satellite sensed sea surface information during the past 10 years has, however, allowed a great push forward, and there is increasing attention to the vast array of fronts and eddies in the open sea.

Our research on the spawning grounds of European eel contributed to basic understanding of the hydrographic processes related to oceanic fronts and of the currents of potential importance to the dispersal and drift of eel larvae. In the 2007 study [20] our measurements using an ADCP (Acoustic Doppler Current Profiler) showed a complex current pattern in the STCZ and hence, in the distribution area of the eel larvae (Fig. 19). The strength and directions of flow changed across the entire STCZ and also varied down the water column. The currents were obviously related to the significant eddy formation in the STCZ, but the observations also indicated strong northeasterly surface currents in the frontal areas where high densities of eel larva were seen.

This important observation pointed to an alternative to the common belief that larvae of European eel initially drift westwards into the Gulf Stream at then drift toward the east. The alternative would be that the European eel larvae take advantage of the front-related surface currents and straightaway drift eastward from the early nursery areas in the STCZ. While many oceanographic models on larval drift from the Sargasso Sea (e.g. Kettle & Haines 2006, Bonhommeau et al. 2009) show a route with initial westward drift, such pattern is not in accord with historical catches of eel larvae across the Atlantic Ocean (Miller et al. 2014). Further, the models initially drifting larvae westward estimate a drift duration of 2 years, which is not in accord with the ageing of larvae reaching the European coasts (Arai et al. 2000).

The realization that the nursery area of Atlantic eels is in a very dynamic area of prominent fronts and eddies, challenges the use of ‘traditional’ oceanographic models using general flow of deep-reaching currents to describe what takes place in the upper 200 meters of a 5000 meter water column. The nursery area is greatly influenced by its prominent eddy formation, and a 2014 research program pursuit new understanding of the role of these eddies in the aggregation and dispersal of eel larvae (B. Nardelli, unpubl.). By use of new oceanographic models incorporating mesoscale eddy processes

we hope to be able to find support for the proposed eastward drift route of European eel; this work is in progress (2015).



An European eel larvae (*A. anguilla*) stretched out on a ruler.

Eel larvae are special in many ways, also in their morphology. All eel species have a leptocephalus stage with a little head, protruding teeth and a laterally compressed body. During growth they build huge amounts of an inert gelatinous material known as glycosaminoglycan (GAG) in their body cavity, and become large and transparent. Photo Sune R. Sørensen

6 SYNTHESIS AND PERSPECTIVES

This final chapter first sums up the descriptions of larval fish ecology presented in Chapters 2-5, taking themes across scales to illustrate the importance of gaining information on a wide range of dimensions (Section 6.1). Subsequently, I conclude what were the major advances in understanding obtained from the studies, setting them in the contexts of the member/vagrant and niche concepts (Section 6.2). Finally, inspired by key observations, I propose specific bio-physical linkages of importance to larval ecology and describe my view of current and future progress within the field of research (Section 6.3).

6.1 Summary - across scales

In the presentations above, the focus was on comparing species and ecosystems, while the wide range of spatial scales used in investigations was apparent in the consecutive presentations of observations and measurements. Those ranged from observations of individual larvae in laboratory experiments to multi-kilometer surveys of wide-spread larval fish populations. The fundamental processes of feeding, growth and disper-sal/drift were the overall research themes, and with each change of scale new facets were added to the picture. With further reference to the scales of observations and processes illustrated in Fig. 1, this summary will emphasize the scale aspects within each theme.

Scale aspects of feeding studies

Centimeters

The shortest scale concerned larval reactions to prey. Distances were in centimeters, while temporally the scales were seconds or minutes. On these scales feeding was studied by direct, visual observations of larval behavior. Fish larvae regulated their prey search intensity according to their experience of prey density, prey size and sense of hunger. The larger the prey, the easier to perceive but the more difficult to catch; thus, to larvae there must be an optimal prey size determined by the balance between visibility and catchability. These aspects were apparent from the observed increase in larval distance of reaction and decline in attack success at increasing prey sizes.

Meters

An intermediate scale could be the distance within reach of larval swimming. This is thus a scale of meters, and temporally the scale is minutes and hours. These scales are mainly of importance for interpretation of processes in the water column.

At this scale we examined the relationship between larval size measures (e.g. length, mouth gape) and the optimal prey size by stomach investigations of field sampled larvae These observations were described by a simple model in which the optimal prey size was a fixed proportion of larval size and the relative width of the prey-size spectrum was constant during larval growth. We found that larvae of different species differed substantially in their prey species preferences. Studies of larval vertical distributions and their feeding in the water column illustrated that larvae prefer certain species assemblages of prey, a preference to some extent based in the respective vertical distributions of both larval and prey species.

Kilometers

The largest scales relate to larval population distribution. On these multi-kilometer and days-to-months scales, we investigated the overlaps of larval distributions with those of their preferred prey (in abundance and type). We demonstrated the importance of fronts as nursery areas for fish larvae, and illustrated how mixing that upwells nutrients leads to enhanced primary production and potentially greater plankton populations to provide larval food. The studies point to the importance of considering not just total zooplankton abundance, but the abundance of preferred prey of the considered larval group. Peak abundances of larvae and prey often coincided or were close to each other in frontal zones. However, across areas and years the degree of overlap between larvae and potential prey varied greatly, and situations appeared when cohorts of larvae did not find sufficient amounts of the preferred prey.

Scale aspect of growth studies

Centimeters

The smallest scales for the growth studies were those used in laboratory experiments. Larvae were reared at the centimeter-scale of experimental tanks, which allowed well-controlled conditions when evaluating growth performance under clearly defined circumstances. Larvae have high growth efficiency, and the experiments showed good capacity for transforming food to growth. High growth rates were achievable in these laboratory studies even at relatively low prey densities, and a comparison to obtainable growth rates in the field suggests that larvae are capable of vigorous growth at the average prey densities generally observed in the field.

Meters - Kilometers

During field studies the trajectories of daily growth were followed from variation in the ring patterns in their otoliths, and our findings illustrated wide individual variation. We found large differences in growth rates between larvae in a cohort according to their position in the frontal zone. On the multi-kilometer-scale of populations, growth variation is important for understanding larval survival and dependence upon environmental factors. Studies on growth/ mortality relationships sug-

gested that relatively faster growth of an individual larva within a cohort will provide it relatively higher survival probability than the average for that cohort.

Scale aspects – swimming, dispersal and drift

Centimeters

At the scale of centimeters, we investigated the swimming behavior of larvae. At low prey densities, or with suboptimal prey sizes, the larval swimming was primarily straight on, interpreted as searching for new areas with improved feeding conditions. On the other hand, when larvae had already found good prey availability in their surroundings their swimming included much more turning, leading to intensified search within the immediate neighborhood.

Meters

At the meter scale of the water column, we examined the migratory behavior of the larvae and interpreted this as active searching for depths with optimal feeding conditions. The importance of light for the visually based search was apparent: larvae migrated to the surface when light diminished at dusk in order to take advantage of the last possibilities for visual feeding, while after the onset of feeding in the surface at dawn, they followed the descent of illumination to a preferred depth where feeding conditions apparently were the best. Such a pattern is also in accord with the observed changes in patchiness of larvae, which were more aggregated near noon.

Kilometers

At the large, multi-kilometer scale we investigated larval drift patterns and found the drift in many respects linked to the physical processes in hydrographic fronts. Effects of converging currents, eddy formation and currents were apparent. We often found the majority of larvae in central areas of the frontal zone where a jet current develops. The dispersal of larvae was ascertained by recurring surveys of larval cohorts and subsequent assessment of distributional changes, and we found the degree of dispersal of larvae to be less across than along fronts. Observed species-specificity in larval vertical distributions, indicate substantial species related differences in drift trajectories.

6.2 Conclusion, fish larval niches and habitats

While significant morphological changes take place during the larval stage, and while all adult characteristics are not obtained until after metamorphosis, there has been a tendency to view larvae as “incomplete”, at the mercy of a harsh and hostile environment. This attitude to fish larvae is changing, and the present observations support a much more comprehensive view of larval skillfulness and capabilities. With respect to their feeding, I found them well-adapted, prepared to meet the challenges involved in

prey search and consumption in a heterogeneous plankton environment. Larvae showed great flexibility, and their reactions were directed by both perception of the environmental conditions and previous feeding history, the latter probably mediated by the sense of gut fullness. Indirect information on feeding behavior gained from observations of their movement in the water column, and a registration of their prey intake, indicate an advanced larval reaction to the environmental challenges, larvae searching for an optimal compromise among a multitude of environmental factors. The main driver would be a desire to maximize prey intake and subsequent growth, but model studies point to the possible additional influence from a drive to avoid predators and/or influence net drift and dispersal (e.g. Fiksen et al. 2007).

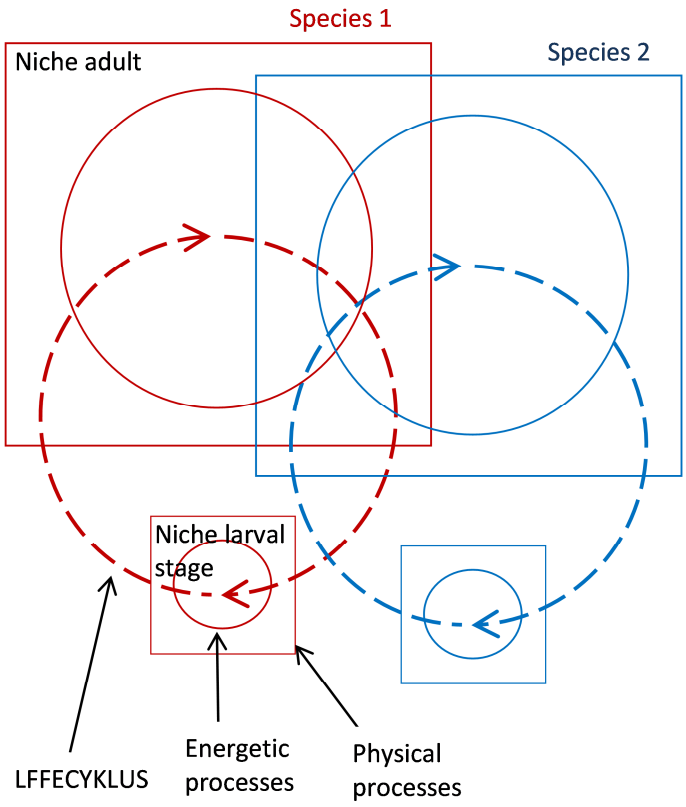


Figure 21. Conceptual illustration of the niches during the life cycle of fishes.

The niches of a given larval and a given adult stage of fish are drawn for two species (blue and red) Energetic processes are indicated as embedded in the physical. Only two niches per species are drawn, but several niches could be described along the fish's lifecycle (hatched line). The niches would be realized in the habitats that fulfill the demands of the given niche. The relatively smaller size at the larval stage illustrates that this niche has more critical demands than the other stages, that this stage is a kind of bottleneck in the lifecycle. The lack of overlap between the two larval niches illustrates that these are strictly species-specific and more difficult to match with appropriate habitat.

Thus, larval adaptability is basically described by the larva's immediate skillfulness (e.g. in their orientation, prey intake, swimming) and its talent for optimal positioning in the three dimensional realm. In Section 1.2 I introduced the niche concept and its potential applicability for the discussion of the relationship between skills, demands and possibilities, and in the following I use that terminology in the further interpretation of observations made during the present studies. A simple, schematic illustration of the larval niches in the life cycle of fish is given in Fig.21.

I interpret the observed structuring in the distribution of species in the frontal zone to represent a strong specificity of their respective niches. This appears from the measured differences of physics and chemistry at respective positions of species in the vertical and horizontal and from the observed differences in their diet. The habitats in which the larvae of different species are distributed are remarkably close to each other, seen in relation to the strong mixing processes, to the dynamic nature of the fronts/eddies and to the massive scale of the open sea. The possibility of being in such close neighborhood could be understood in a three-dimensional view through which a varied set of possible habitats appear available to fulfill a range of distinctive niche demands. Further, many factors and processes must be inter-related. For example, our findings indicate that habitats of certain species of fish larvae clearly overlap with habitats of certain species of copepods. Thus, these very dissimilar organisms not only are linked in the food chain context (the copepod being prey of the larva), but share fates as both depend on the dynamic physical habitat where conditions could change to better or to worse.

We might expect a certain degree of plasticity of the niche. Poor conditions along one niche dimension could be counterbalanced by better conditions along another, and fish larvae could adapt to habitat changes by moving distances within their swimming range. On the larger scale (kilometers, months) there might, however, be an unavoidable risk for a failure in the overlap between niche and appropriate habitat. This is exemplified by occasions of larger cod larvae not being able to satisfy their need for larger prey organisms in specific areas of the North Sea, indicated by comparative observations in in the present study, and by the study by Beaugrand et al. (2003) who used a time-series of cod larval survival estimates and abundances of larger prey organisms (*Calanus* sp.).

On the time scale of evolution an overlap between niche and appropriate habitat would be of ultimate importance. A specific minimum of successful acquisition of niche demands over time would be necessary. The result of our investigations on linkages between larval fish ecology, their nursery areas and the performance of hydrographic fronts (and comparable hydrographic features) indicates that it might not only be the low-dispersal physical properties of the fronts that direct the process of selection. In addition, the environmental diversity and unique productivity of fronts would be of

importance. Many of the characteristics of fronts are apparent in the comparative analysis, which has included a wide range of frontal types in different climate zones. We did not find fronts to be single, uniform units, but instead to be diverse *frontal zones* across which there is a wide range of different habitats to fish larvae and other plankton organisms.

Recently there has been further emphasis placed on the importance of fronts, eddies and upwelling areas for reproduction of fishes (e.g. Belkin 2009, Bakun 2006, 2010). Not only the possible retention and guidance of larval drift by fronts are in focus, but also the importance of an enhanced biological production and of plankton concentration (cf. Ocean Triad Hypothesis, Bakun 2010). In accordance with the findings of the present studies, there is now accumulating evidence of universal bio-physical linkages in the larval fish nursery areas, and there is a move toward integrating several aspects of fronts, eddies and upwelling areas, with increased focus on how these create habitats satisfying numerous distinct niches for fish larvae.

Leptocephali of eels

There are many other eel species in the Sargasso Sea than the European and the American eel. In this dish we show a variety of species in the leptocephali stages of eels. Some species can be up to ½ meter long during this stage, still having quite small heads. Lengths of the larvae here are about 10 cm.

6.3 Ideas and perspectives

Focus on influence from neutral buoyancy

In this final section I will devote some space to elaborate on a hypothesis dealing with bio-physical linkages of potentially great influence to larval ecology, proposing relationships that in my opinion are much overlooked in this research field.

During my field research I have always found the recurrent structuring of fish larval assemblages and the close neighborhoods of species habitats astonishing, and have not found this well explained by current hypotheses. Thus, how is it possible for larvae of different species to establish and sustain distinct relative positions within nursery areas, i.e. the frontal zones? There might be more of both passive and active tools, in the tool chests of larvae than we have yet identified. The present studies have pointed out the advanced and complex behavior of fish larvae. For example they show multi-facetted reactions in relation to the character and density of prey and to physical conditions such as light and turbulence. These behaviors allow them the capacity to find specific conditions in their near environment. However, these conditions do not appear sufficiently stable and delimited in time and space to sustain the observed degree of separation between species. Thus, while a characteristic of frontal zones is prominent gradients in physics and chemistry, the question arises whether fish larvae could orient themselves in relation to combinations of them. Many examples are seen of fish orienting to temperature gradients (Beitinger 1990), but temperature is quite unstable, changing during the day and over seasons. Salinity is much more stable through time, and it does have obvious importance in the osmoregulation of fish. However, a search based on gradients of osmotic stress does not appear as a suitable way to sustain spatial differentiation in species distributions..

A possible relationship to physics/chemistry might be found in the buoyancy effect. It is a common observation that many marine pelagic organisms seek to be neutrally buoyant in their immediate surroundings (Phleger 1998). Several of the constituents of fish are heavier than the surrounding seawater, and a range of strategies have been developed to avoid sinking. For example, they can have a low content of the heavy ions, a high water content or high fat content, and many can develop a swim bladder (Phleger 1998). A major advantage of being neutrally buoyant is that very little energy is used for keeping the position in the water column, and attacking prey would be much easier when the fish does not need to counterbalance up- or down-directed forces during the attack. The question arises, do larvae have characteristic buoyancy differences among species and are buoyancy effects sufficient to direct their positions in the chaotic stirring of frontal zones?

Several studies demonstrate close equivalence between the material density of eggs from a given species and the water density at their position in the water column (Ådlandsvik et al. 2001, Boyra et al. 2003, Coombs et al. 2004). Sclafani et al. (1993) found that specific characteristics of larval buoyancy, related to e.g. larval size and condition, explain observed vertical distributions and migrations, patterns that might strongly influence their drift and retention. Cod larvae are well studied in this regard, and our studies showed good agreement between the laboratory-measured estimates for larval neutral buoyancy (at salinity of 34.5 pss, Ellertsen et al. 1980) and salinity at the observed average depth of larvae (34.6 pss, [21]). Of special interest for this relationship is the horizontal variation of salinity and water density across frontal zones. In the horizontal dimension there are large areas where water density is the same through most of the water column. These could be optimal habitats for fish larvae with density appropriate for neutral buoyancy in the area.

Such potential link between distributions of fish larvae and a specific chemical parameter could contribute to interpretations of larval fish ecology related to the member/vagrant concept. While this hypothesis has great focus on potential losses from the population, and therefore on frontal physical processes that diminish dispersal, it does not take into account the recurring structuring of species assemblages within the frontal zone. The potential selection against dispersal should work for all species, and selection for different degrees of dispersal is not likely. On the other hand, there might be selection for fitting as many species as possible into the beneficial habitat characteristics of frontal zones. Selection for linkage to a given conservative, measurable and beneficial characteristic like salinity could be the basis for the structuring of fish larval assemblages. In these, niche separations should be sufficient to separate species and/or populations, with each sub-habitat linked to a specific drift pattern (life cycle closure) and the front ensuring a generally restricted dispersal to all.

Future prospects

New findings and methods are contributing to the continued search for better understanding of niche separation among plankton organisms. The present findings of advanced skills for orientation and reaction are being supplemented by new studies of larval behavior providing new insight on fish larval capabilities. These studies show directional swimming of larvae in relation to multiple physical/chemical cues, e.g. to pheromones (Paris et al. 2013), magnetic field variations (Nishi et al. 2005), sound (Montgomery et al. 2006) and sunlight (Leis et al. 2014). This new information on larval behavioral decisions constitutes a major step forward in the interpretation of larval dispersal and population connectivity (Cowan and Sponaugle 2009). We are gathering further evidence of directional behavior of larvae in the vertical dimension,

movements by which they actively use the current variability in the water column to influence dispersal and drift. This is a very encouraging aspect within the research field.

Several of these recent investigations of larval behavior have been carried out *in situ* on fish larvae at coral reefs, and have been inspired by new findings on the genetics of reef-fish metapopulations and the degree of connectivity among subpopulations (e.g. Hogan et al 2012). The use of genetic (molecular) techniques in marine research is expanding and new understanding of the character of sub-population structures, obtained from the genetical information, is another great incentive to larval fish research. Generally, the genetic methods have shown to be of great value for research in population structures and life cycles (e.g. Galarza et al. 2009). The technique can be used for quite different purposes as I have experienced lately during the processing of samples from two Sargasso Sea cruises. Here we used the so-called DNA-barcoding technique for identifications of hitherto unidentifiable larvae (Ayala et al. 2016) and we are in the process of further genetic-based identification of eel larvae stomach contents (Ayala et al., in prep). The genetic research on sub-population structures as for example of cod and Atlantic herring (Hutchinson et al. 2001, Limborg et al. 2012) is of great potential. A range of specific molecular techniques will certainly become standard tools for larval fish researchers and will in the future – combined with solid empirical research and oceanographic modelling - contribute substantially to our increasing understanding of the life of fish larvae and their role in population formation and variation.

Larva from the tropics

Larvae inevitable die after catch and quickly lose their colors and shape. In a few cases it has been possible to get hold of larvae and picture them live in their colorful stage. Here I was lucky and grasp the beauty of a live larva caught off Broome, Australia.

Photo P.Munk.

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